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No. 1

THE VEGETATION OF THE CADDO COUNTY CANYONS, OKLAHOMA

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An unusual eastern deciduous forest, in which sugar maple, *Acer saccharum* Marsh., is dominant and disjunct at the extreme western limit of the species, is present in four canyons in Caddo and Canadian counties, west central Oklahoma, 175 miles west of the typical range of this forest type in eastern Oklahoma. These sandstone canyons and their vegetation resemble in several ways the better known sandstone canyons in Starved Rock State Park, Illinois. The author made many field trips to the Caddo County canyons from 1930 to 1933 and a final trip in September, 1936, to complete this study.

DESCRIPTION OF THE CANYONS

The largest and best known of these canyons are located in northern Caddo County and southwestern Canadian County near the town of Hinton and include Devils, Kickapoo, South, and Water Canyons. Smaller canyons without sugar maples are found in several adjacent counties.

These canyons have been cut in the Whitehorse formation, which is a soft or poorly cemented, massive, red sandstone of the Permian "Red Beds." Along Oklahoma's major stream divide at an elevation of about 1,500 feet, the canyons have been carved back by tributaries of the South Canadian River on the north and by tributaries of the Washita River on the south.

The largest canyons are a few miles long and 100 to 200 feet deep. They are broadly "U" shaped and have soil bottoms averaging 300 feet across and bordered by vertical red sandstone cliffs 30 to 70 feet high (fig. 1). Above these rock walls the less resistant rock formations have weathered to form gradually widening, soil covered, vegetated slopes. The smaller canyons and upper ends of larger ones are narrowly "U" shaped with rock bottoms and sides.

¹ Maintained at Tucson, Arizona, by the U. S. Forest Service in cooperation with the University of Arizona.

Small permanent streams of the largest canyons, which are fed by springs along the bases of the cliffs, have banks up to 10 feet apart. Having almost reached base level, the streams meander in wide curves across the floors. Where intermittent tributaries enter the tops of the cliffs to form temporary water falls during rains, there are formed slightly rounded overhanging walls.

Vegetation in the canyon bottoms has enriched the soils by addition of humus. Soil moisture is high and the water table is shallow, in contrast to conditions at the tops of the canyons.

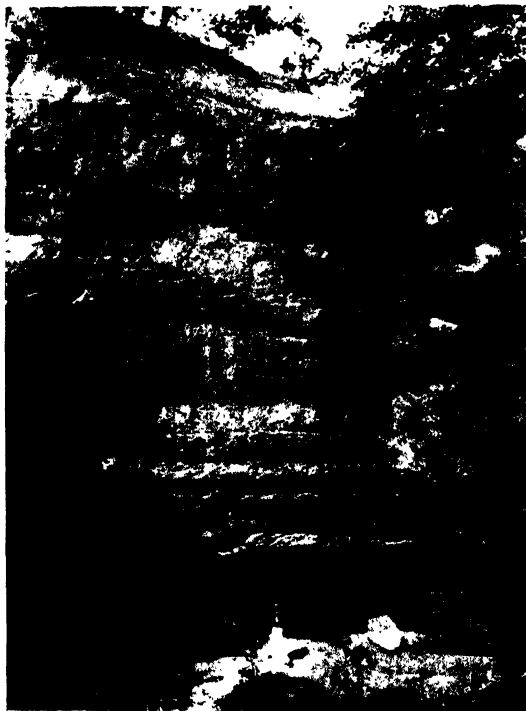


FIG. 1. Overhanging, rounded wall of Devils Canyon where a tributary enters. Sugar maple tree at right.

Annual precipitation in this area is about 30 inches. The canyons are sheltered from the strong, drying winds on the exposed upland nearby. Light is reduced by shade of the vertical walls and the dense canopy of trees. Evaporation is much lower and temperatures less extreme in the canyons than in the adjacent upland.

UPLAND VEGETATION AT TOP OF CANYONS

In the forest-grassland transition zone where the Caddo County canyons are located, the forest occurs generally on soils derived from sandstone and

the prairie on soils underlain by shale. The prairie of the upland here and westward is the typical *Andropogon* tall-grass climax association, which has been destroyed in most places by cultivation or overgrazing. In the undisturbed prairie here prairie beardgrass, *Andropogon scoparius*, is the dominant species. Plants of *A. hallii* are common also and rarely reach a height of 8 to 9 feet near the canyons. Grasses, legumes, and composites are common and include: *Elymus canadensis*, *Amorpha canescens*, *Tephrosia virginiana*, *Lespedeza frutescens*, *Artemisia kansana*, *Chrysopsis villosa* var. *stenophylla*, and *Gaillardia fastigiata*. Also represented are *Yucca glauca*, *Paronychia wardii*, and *Salvia azurea* var. *grandiflora*.

In most places, however, the upland prairie above the canyons has been severely overgrazed. The tall grasses have been succeeded by a ruderal association of unpalatable herbs and short grasses, the dominant species being *Ambrosia psilostachya*, *Eriogonum annuum*, *Bouteloua hirsuta*, and *Festuca octoflora*. Other ruderal species less commonly represented here are: *Baptisia bracteata*, *Stillingia sylvatica*, *Vernonia baldwinii*, *Opuntia engelmannii* and *O. humifusa*.

The oak woodland, or *Quercus marilandica* climax association, borders the canyons on the adjacent upland, where it is at the western limit of upland forests in this part of the state. In this open, dwarf woodland blackjack oak, *Quercus marilandica*, is the dominant species. Other characteristic species are eastern red cedar, *Juniperus virginiana*, and post oak, *Quercus stellata*, trees averaging only 10 to 15 feet high and 4 to 6 inches D. B. H. In openings between the scattered dwarf trees occur herbs of the prairie and ruderal associations, also a few shrubs of *Prunus gracilis*, *Rhus glabra*, and *R. trilobata*.

VEGETATION OF THE CANYON BOTTOMS

Sugar maple forest

In passing through the xerophytic oak woodland or overgrazed prairie to the precipitous rock wall of Devils Canyon, one looks into a luxuriant deciduous forest. As the sugar maple is the dominant species, this forest may be designated as the *Acer saccharum* association, which is an edaphic climax or postclimax. This deciduous forest is characterized by large, tall, straight trees averaging 1 to 2 feet D. B. H. and 50 to 70 feet in height and forming a closed canopy (fig. 2). Nearly half the trees in this association are sugar maples, which reach a maximum size of about 27 inches D. B. H. and 75 feet in height (fig. 3). Not only are mature trees common, but seedlings and all stages of reproduction of sugar maples are also numerous. Some of the trees have been tapped locally for sugar.

Other trees most commonly represented in this association are: *Acer negundo*, *Juglans nigra*, *Ulmus americana*, *Celtis occidentalis* var. *crassifolia*, and *Quercus shumardii*. In smaller canyons where sugar maples are not found, trees of these species are characteristic.

Because of the shade of the dense canopy, plants in the undergrowth are not numerous. The shrub most commonly represented is *Symphoricarpos orbiculatus*, bushes of which average 2 to 3 feet in height. Lianas are well represented by *Menispermum canadense*, *Rhus toxicodendron*, *Parthenocissus quinquefolia*, *Vitis cordifolia*, and six additional species.

Herbs are not abundant, but a few species are fairly common. The characteristic spring flora includes: *Carex* spp., *Polygonatum commutatum*, *Sisyrinchium gramineum*, *Claytonia virginica*, *Thalictrum dasycarpum*, *Viola missouriensis*, and *Galium aparine*. In summer, other herbs are conspicuous such as: *Bromus purgans*, *Elymus villosus*, *E. virginicus*, *Leersia virginica*,



FIG. 2. *Acer saccharum* association of large trees in Kiwanis Park, South Canyon.

FIG. 3. Trunk of a large sugar maple in Devils Canyon.

Uniola latifolia, *Parietaria pennsylvanica*, *Boehmeria cylindrica*, *Laportea canadensis*, *Pilea pumila*, *Polygonum hydropiper*, *P. virginianum*, *Phytolacca americana*, *Euphorbia heterophylla*, *Cryptotaenia canadensis*, *Sanicula canadensis*, *Aster drummondii*, and *Bidens bipinnata*. On sloping sandy soil banks slightly above the level of the forest floor the moss *Mnium cuspidatum* forms large mats.

In a few openings on higher levels with drier soils and in cleared areas, shrubs of *Rhus glabra* 3 to 10 feet high are pioneers. On cleared portions of South Canyon and Devils Canyon are good pastures of Bermuda grass, *Cynodon dactylon*. *Ambrosia psilostachya* is invading in a few places as indicator of overgrazing.

Streams and springs

There is a slight difference in the vegetation along borders of the small streams in the canyon bottoms. *Cephalanthus occidentalis* and *Equisetum praealtum* grow at the edge of the water, while in the dense canyon bottom forest, *Populus deltoides* and *Salix nigra*, are rare and occur only at the edge of streams; they become common in openings and cleared areas.

The few springs at bases of sandstone cliffs are bordered by rather moist soils which have a few hydrophytes including mats of *Conocephalum conicum*. Herbaceous species typical of these moist sites, are: *Muhlenbergia schreberi*, *Iresine paniculata*, *Radicula nasturtium-aquaticum*, *Samolus floribundus*, *Lobelia cardinalis*, and *Elephantopus carolinianus*.

Canyon walls

The vertical sandstone canyon walls have an interesting vegetation of pioneer plants which vary from top to bottom. As trees shade the walls, the direction to which the wall faces has only slight effect on the vegetation except in cleared areas. Lichens, liverworts, mosses, and ferns occupy the rock walls, where seed plants are less able to get established.

On the sloping top of the rock canyon wall the pioneer vegetation is usually a mat of *Selaginella sheldoni*. With it are xerophytic mosses, such as *Weisia viridula* and *Tortula ruralis*, and lichens of several species. Where there is a small amount of soil at the top may be found the next stage, scattered plants of *Juniperus virginiana*, *Andropogon scoparius*, *Yucca glauca*, *Quercus marilandica*, and *Opuntia engelmannii*.

The dry vertical canyon walls are mostly barren except for a coat of crustose lichens and a few foliose lichens. Where portions of the rock have broken off recently even lichens are absent. In a few places vines of poison ivy, *Rhus toxicodendron*, climb the walls from bottom to top.

The moist portions of shaded canyon walls have richer vegetation. Where water runs down the walls during rains from intermittent streams above, there are more lichens and xerophytic mosses. In crevices a few ferns such as *Asplenium platyneuron*, *A. resiliens*, *Cheilanthes castanea*, *Pellaea atropurpurea*, and *Woodsia obtusa* may be found. On slightly moist, shaded walls at top and bottom liverworts of the species *Reboulia hemisphaerica* form mats.

Where the walls are kept moist by springs or by streams *Conocephalum conicum* is common and forms mats up to a height of about 3 feet above the base. Two additional ferns, *Cystopteris fragilis* and *Adiantum capillus-veneris*, are restricted to these moist, perpetually shaded habitats, where they are rare.

Recent changes in the canyons

Certain disturbances caused by man are beginning to show their effects in the canyons. The lower, broader parts have been cleared and changed into

cultivated fields and pastures. There has been some grazing by cattle and cutting of trees for fuel. It is said that a sawmill cut out the larger black walnut trees in Devils Canyon about 30 years ago.

Accelerated soil erosion on the watersheds above the canyons due to cultivation and overgrazing has resulted in rapid deposition of sand on the canyon floors by flood waters with burial of rich soil and destruction of herbaceous vegetation. During one heavy rain in 1933 a layer of sand nearly 1 foot deep was deposited on a small area of Devils Canyon.

Due to increased volume of flood waters and load, the meandering stream of Devils Canyon has eroded, widened, and deepened its channel with some destruction to the bordering vegetation. Even large trees, a foot in diameter, have been uprooted at various places along the stream bed within the past few years. On the inner curves large banks of sand have been deposited. These changes apparently are far greater than any that may have occurred in these canyons in hundreds of years.

Efforts should be made at once to preserve one of these canyons with the watershed above as a state park or other public-owned area for benefit of future generations. Fortunately, a portion of South Canyon, although disturbed by some clearing, has been developed by a Hinton civic club as Kiwanis Park.

WOODY PLANTS OF THE CADDO COUNTY CANYONS

No thorough list of species of seed plants of these interesting canyons has been prepared. The author's ('36a, '36b) lists of 10 liverworts, 54 species of mosses, and 11 pteridophytes from a slightly larger group of west central Oklahoma canyons demonstrate the relative richness of these plants in the canyons. Lichens and fungi apparently are common also and numerous in comparison with the surrounding territory.

Specimens of the relatively large number of woody species of the canyons were collected by the author and deposited in the herbaria of the Arnold Arboretum and the University of Oklahoma. The author is indebted to Alfred Rehder and Ernest J. Palmer, of the Arnold Arboretum, for checking his determinations of certain specimens. The lists that follow contain 54 woody species, including 27 species of trees, 17 of shrubs, and 10 of woody vines. Eastern species that are at or near their western limits in these canyons, although some may occur farther southwest in the Wichita Mountains also, are indicated by an asterisk (*) in the lists. Phillips and Gould ('32) reported from these canyons two additional tree species, *Juglans rupestris* and *Diospyros virginiana*.

The outstanding plants of these canyons are the trees, which are high in number of species for this part of Oklahoma and also of relatively large size. The largest measurement of diameter breast height of trees of each species observed in Devils Canyon is given in inches. Although not measured ac-

curately, heights of the largest trees of each canopy species are about 50 to 90 feet.

Tree species typical of canyon bottoms

- Juniperus virginiana* L. To 10.5 inches d. b. h. and 40 feet in height. One stump was 18 inches in diameter. Also at tops of canyons.
Populus deltoides Marsh. To 32 inches.
Salix nigra Marsh. To 12 inches.
Juglans nigra L. To 28 inches. One stump was more than 4 feet in diameter.
Quercus macrocarpa Michx. To 40 inches.
Quercus muhlenbergii Engelm. To 37 inches.
**Quercus shumardii* Buckl. To 33 inches.
Ulmus americana L. To 34 inches.
Ulmus fulva Michx. To 21 inches.
**Celtis laevigata* Willd.
**Celtis occidentalis* var. *crassifolia* A. Gray. To 26 inches.
Morus rubra L. To 13 inches.
Prunus mexicana S. Wats. To 13 inches and 30 feet in height.
Cercis canadensis L. To 11.5 inches and 30 feet in height.
Gymnocladus dioica K. Koch. To 5 inches and 30 feet in height.
Acer negundo var. **texanum* Pax. To 24 inches.
**Acer saccharum* Marsh. To 27 inches and 75 feet in height.
Sapindus drummondii Hook. & Arn. To 8 inches. In more open places.
Bumelia lanuginosa Pers. To 18.5 inches and 90 feet in height. Unusually large for trees of this species.
Fraxinus pennsylvanica var. *lanceolata* (Borkh.) Sarg. To 8 inches.
**Viburnum rufidulum* Raf. To 3 inches and 15 feet in height.

Tree species typical of other habitats

- Salix longifolia* Muhl. Moist soils at open lower ends of canyons.
Quercus marilandica Muench. Oak woodlands at tops of canyons.
Quercus stellata Wang. Oak woodlands at tops of canyons.
Celtis reticulata Torr. Oak woodlands at tops of canyons.
Morus alba L. Escaped from cultivation at lower end of a canyon.
Catalpa bignonioides Walt. To 6 inches and 30 feet in height. Escaped from cultivation in Devils Canyon.

Shrubs and woody vines typical of canyon bottoms

- Ribes aurum* Pursh.
Rubus flagellaris var. *occidentalis* Bailey.
Rhus glabra L., pioneer in openings and clearings.
Evonymus atropurpureus Jacq.
Aesculus glabra var. *sargentii* Rehd., also on uplands.
Cornus asperifolia Michx.
Forestiera pubescens Nutt.
Cephalanthus occidentalis L.
Sambucus canadensis L.
Symphoricarpos orbiculatus Moench.
Smilax bona-nox L. and *S. hispida* Muhl.
Cocculus carolinus (L.) DC.
**Menispermum canadense* L.
Rhus toxicodendron L.

Celastrus scandens L.

Parthenocissus quinquefolia (L.) Planch.

Cissus ampelopsis Pers.

Vitis cordifolia Michx. and *V. linsecomii* var. *glauca* Munson.

Shrubs typical of uplands

Yucca glauca Nutt.

Prunus gracilis Engelm. & Gray.

Amorpha canescens Pursh.

Prosopis juliflora var. *glandulosa* (Torr.) Cock., one plant perhaps adventive near top of Water Canyon.

Rhus trilobata Nutt.

Opuntia engelmannii Salm-Dyck and *O. humifusa* Raf.

RELATIONSHIPS OF THE FLORA OF THE CANYONS

Distribution of Acer saccharum

The flora of the Caddo County canyons presents problems in geographic distribution of species, of which the disjunct distribution of sugar maple is the principal one. The tree is present in four canyons in Caddo and Canadian counties as disjunct patches at the westernmost point of the range of the species (exclusive of *Acer saccharum* var. *sinuosum* in southwestern Texas) along its entire broad western border from Manitoba to Texas. Specimens have not been collected nearer these canyons than 175 miles eastward, in eastern Muskogee County.

The natural, continuous range of *Acer saccharum* extends into eastern Oklahoma about 50 miles west of the Arkansas line, both in the Ozark plateau of northeastern Oklahoma and in the Ouachita Mountains of the southeastern part of the State. In McCurtain County in the Ouachita Mountains the author has collected specimens of the closely related whitebark maple, *Acer leucoderme*, at the extreme western limit of its range in southeastern United States.

Relict flora hypothesis

The most reasonable explanation for the disjunct distribution of sugar maples in the Caddo County canyons is the relict flora hypothesis. During humid periods of various fluctuations in past climates the eastern deciduous forest may have migrated farther west. If so, sugar maples may have had a continuous range westward to these canyons or beyond. With the advent of a drier climate, when plants of the more mesophytic species may have died out along their western limits, islands of certain eastern species, such as *Acer saccharum*, may have remained in these favorable canyon bottoms. Sears ('32, '33) regarded the sugar maples here as relicts of the humid period of 4000 B. C. or of an earlier humid climate. Clements ('36, p. 134) also accepted the relict hypothesis.

No other eastern woody plants in these canyons are definitely known to be disjunct. *Menispermum canadense* perhaps is most unusual in range. On the other hand, certain eastern tree species whose continuous ranges extend farther west in eastern Oklahoma than sugar maple are not represented in these canyons. However, the continuous range of *Acer saccharum* in eastern Oklahoma projects farther westward than do the ranges of tree species, such as *Quercus alba*, *Acer rubrum*, and *Tilia floridana*, of the same forest association there.

Epilobium coloratum Muhl., not previously reported from Oklahoma, is represented on moist soils in Devils Canyon at probably its southwestern known limit. Dr. Milton Hopkins, of the University of Oklahoma, has kindly checked the determination. Careful search may reveal other herbaceous disjuncts.

Herbs of several eastern species here appear to be at or near the western limits of the species in these canyons on the basis of imperfectly known distribution within Oklahoma. A few of these may be disjunct and some are present also in the Wichita Mountains of southwestern Oklahoma. Additional distribution notes on these species have been contributed by Dr. Milton Hopkins. These eastern species are: *Leersia virginica*, *Muhlenbergia schreberi*, *Uniola latifolia*, *Arisacma dracontium*, *Boehmeria cylindrica*, *Laportea canadensis*, *Pilea pumila*, *Polygonum virginianum*, *Passiflora lutea*, *Epilobium coloratum*, *Cryptotaenia canadensis*, *Osmorhiza longistylis*, *Phryma leptostachya*, *Melothria pendula*, and *Elephantopus carolinianus*.

Plants of a few southwestern species, which are at or near their north-eastern limits in these canyons, may have invaded from the west during drier periods. These include: *Selaginella sheldoni*, *Cheilanthes castanea*, and *Husnotiella revoluta* var. *palmeri*.

The Wichita Mountains, located principally in a bordering county, Comanche County, about 50 to 75 miles south and southwest of the Caddo County canyons, have plants of some eastern disjunct species at their western limits also and may contribute toward a solution of plant distribution in the canyons. Although the sugar maple is absent, certain eastern species not found in the canyons occur here.

One of the most unusual disjunct species in Oklahoma is the western, parallel species of sugar maple, the bigtooth maple, *Acer grandidentatum*, represented in the Wichita Mountains at the easternmost limit and only Oklahoma station. This species of higher zones in the Rocky Mountains from Montana to Coahuila is found nearest in mountains of western Texas 400 miles southwest of the Oklahoma location.

These two maples of eastern and western forests thus are separated by only 50 miles and almost meet across the grassland in Oklahoma. Palmer ('34) stated that the presence of *Acer grandidentatum* in the Wichita Mountains "is particularly interesting as indicating a former invasion of Rocky Mountain plants into the region." However, just as *Acer saccharum* has no

disjunct eastern species associated with it in the Caddo County canyons, no distinctly western associated species of range and habitat similar to *Acer grandidentatum* is represented disjunct in the Wichita Mountains.

SUMMARY

Four sandstone canyons near the town of Hinton in Caddo and Canadian counties, west central Oklahoma, have a rich, eastern deciduous forest, in which *Acer saccharum* is dominant and disjunct at the extreme western limit of the species. The surrounding vegetation is transition between oak woodland and tall-grass prairie.

Twenty-seven species of trees, 17 of shrubs, and 10 of woody vines, relatively large numbers for this locality, are represented in the canyons and adjacent upland. Ferns, mosses, liverworts, and lichens are well displayed.

The sugar maples in the canyons 175 miles from the nearest sugar maples in eastern Oklahoma are regarded as relicts of a more humid climate when the eastern deciduous forest probably extended farther west.

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AN ECOLOGICAL STUDY OF THE FRESH-WATER SPONGES OF WISCONSIN, II. THE INFLUENCE OF CALCIUM

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In 1935 the author published the results of her studies on the ecology of fresh-water sponges collected from 103 lakes and 15 streams in Vilas and Oneida Counties in Wisconsin. In continuing these studies an effort has been made to extend the field observations over a wider variety of habitats, and to check conclusions based upon field work by experimental rearing of sponges in chemically modified waters.

These studies were made at the Wisconsin State Biological Survey headquarters at Trout Lake, Wisconsin, during the summers of 1935, 1936, and 1937. All chemical data presented were furnished by Professor C. Juday, director of the Biological Survey, to whom the author is also indebted for the use of the facilities of the station, and for many other courtesies.

FIELD DATA

Table I shows the distribution of Spongillidae in 54 lakes and 9 streams not previously reported. Numerous lakes and streams reported in 1935 were also revisited. In addition to the ten species of Spongillidae reported from Vilas County in 1935, *Carterius tenosperma* Potts has been collected from Spider Lake by Neidhoefer ('38), and *Ephydatia crateriformis* Potts has been found in Stone Lake and a connecting flowage by both Neidhoefer and the author. These, with two species reported from Wisconsin by Smith ('21) but not positively identified in the author's collections, *Ephydatia fluviatilis* (auctorum) and *Carterius latitencia* Potts, make fourteen species of fresh-water sponge known to occur in Wisconsin. Of these species, however, not more than seven or eight occur with sufficient frequency for an ecological study.

The State of Wisconsin lies in three drainage areas. The extreme northern part of the state drains into Lake Superior. The small lakes of this region resemble those of upper Michigan and are of moderate to low calcium content. The larger part of the state drains west into the Mississippi river. The waters of the northern part of this area, including most of Vilas, Oneida, and Lincoln counties, are extremely soft as compared to the waters of the limestone regions in the central and southern parts of the state.

Summit Lake is said to be the highest lake in the State of Wisconsin. In the Summit Lake region, within an area about six miles long and five miles

TABLE I.—Continued

LAKE	Mgms. per liter							Conductivity reciprocal megohms	Residue mgs. per l.	Color	<i>R. malleri</i>	<i>S. fragilis</i>	<i>S. lacustris</i>	<i>T. pennsylvanica</i>	<i>S. engeliformis</i>	<i>H. everetti</i>	<i>H. argyrosperma</i>	<i>H. repens</i>	<i>H. ydleri</i>
	O ₂	Free CO ₂	Bound CO ₂	pH	SiO ₂	Ca	Mg												
MISSISSIPPI DRAINAGE AREA—Continued Oneida County																			
Big Carr.	8.18	2.5	1.0	5.1	0.2	0.85	0.64	12.2	17.2	5				*					
Carroll.	9.0	1.5	23.25	7.6	11.5	13.6	4.0	98.0	80.0	18									
Carroll Bog.			10.2	6.7		4.9													
Kawagagesaga.	9.4	—1.0	18.25	8.1	6.4	11.64	3.25	86.0	58.5	8				*					
Little Carr.	7.9	1.95	1.4	6.5	0.0			10.3	16.4	6				*					
Madeline.	8.8	—0.5	11.87	8.6	3.6	13.7	3.75	90.0	68.0	8				*					
McGrath.	8.1	2.0	1.5	5.3	0.0	0.9	1.25	11.9	18.5	6				*					
Pelican River.		2.5	17.5	7.1	8.3	9.2	5.25	70.0		128				*					
Pier.			9.8	6.8		5.0								*					
Sweeney Lake.	11.4	—3.75	18.25	8.2	4.2	11.52		60.0	66.7	26				*					*
Sweeney outlet.														*					
Tomahawk I.		0.25	15.5	7.7	0.8	7.4	2.61	62.5	46.3	8				*					
Tomahawk River below Lake Kawagagesaga.			19.0	7.2		11.04	4.0							*					
N. of Tomahawk.			19.0	7.2	7.5	11.72	4.0			95				*					
Wisconsin River.		7.0	15.0	6.9	11.6	8.0	3.5	63		78				*					
Lincoln County																			
Black Alder.					2.1	4.72	0.0			138				*					
Prairie River.					10.9	23.08	7.0			35				*					
Road Lake.						6.92	2.25			110				*					

TABLE I.—Continued

LAKE	Mgms. per liter							Conductivity reciprocal megohms	Residue in grms. per l.	Color	B. milleri	S. fragilis	S. lacustris	T. pennsylvanica	S. ingolfiformis	F. everetti	H. argyrops perma	H. repens	H. lyderi
	O ₂	Free CO ₂	Bound CO ₂	pH	SiO ₂	Ca	Mg												
LAKE MICHIGAN DRAINAGE AREA—Continued Head of Wolf River																			
Mole Lake.....	—0.75	8.25	7.1	2.75	4.68	2.0	42	74.9	58	*	*	*	*	*	*	*	*	*	*
Post Lake.....	—2.5	28.0	7.7	6.2	11.95	5.27	94												
Wa bi kon L.....	—9.85	36.6	8.8	20.5	15.4	10.0	135												
Lower Wolf River—Waupaca Chain o' Lakes																			
Bass.....	—8.9	46.9	8.7	7.5	17.3	19.0	180												
Beasley	—6.15	60.15	8.5	8.0	22.0	210													
Drake.....	—5.1	57.0	8.3	4.5	20.8	22.0	205					*							
Knight.....	—6.0	64.0	8.5	7.75	24.6	22.0	225												
Long.....	—4.5	71.25	8.3	7.5	29.7	22.0	255												
Marl.....	2.1	67.6	7.9	8.0	28.6	20.0	250												
Miner.....	—3.9	55.6	8.3	3.75	19.5	22.0	202												
Mud.....	—3.9	66.0	8.3	7.5	27.1	22.0	240												
Otter.....	—6.2	65.5	8.5	7.5	24.4	22.0	245												
Pope.....	—5.4	66.5	8.0	9.0	27.6	20.0	240												
Rainbow.....	—6.5	55.7	8.3	4.0	19.4	20.0	200					*							
Round.....	—7.0	56.75	8.6	4.25	20.0	18.0	205												
Young.....	—4.5	54.15	8.5	7.75	16.0	205													*
Emmons Creek.....	—1.5	84.85		12.0	42.0	26.0	300												

wide, are over thirty lakes, some of which drain east through tributaries of the Wolf River, others of which drain to the south and west through the EauClaire and Pine Rivers, while still others drain to the north and west through the Prairie River. Although varying somewhat among themselves, all of the lakes of this group yet studied are soft-water lakes.

Passing south and east from Summit Lake, one enters an area underlain by Niagara limestone, and drained into Green Bay through the Oconto and Wolf rivers. The waters of this region are extremely high in both calcium and magnesium. Of the lakes examined, only Mole and Post Lakes, at the very head of the Wolf River, were without deposits of marl or travertine, thus the waters examined during this study include the entire range of calcium and magnesium content from practical absence to supersaturation.

The sponges collected from Vilas and Oneida Counties (Table I) add little to the range of ecological conditions already reported for the various species (Jewell, '35). The finding of *Ephydatia everetti* (Mills) in Deadwood Lake, Color 65, is the first report of this species from a water high in color. It is worthy of remark that these specimens were found on arctic moss and twigs in depths of from about $\frac{1}{4}$ to 1 meter, in contrast to the depths of $1\frac{1}{2}$ to $3\frac{1}{2}$ meters at which this species has been found in transparent waters. Morton Lake, with a free CO_2 content of 14.5 mgms. per liter and residue of 97, increases the range of these two conditions from which the author has collected *Ephydatia mülleri* (Lieberkuhn) and *Spongilla fragilis* Leidy.

Since Wildcat Lake, with a bound CO_2 content of 29 to 32 mgms. per liter, Ca 18.8, and conductivity 118 reciprocal megohms, was the most highly mineralized water examined by the author in 1935, the data here presented from the Lake Michigan drainage area decidedly increases the known range of sponge distribution with regard to certain factors. Old ('32) reported *Spongilla fragilis* and *S. lacustris* from waters having methyl orange alkalities as high as 170 mgms. per liter calcium carbonate (the equivalent of a bound CO_2 content of 74.8 mgms. per liter) which is a higher concentration of carbonates than any from which the author has collected these species. The conductivity of Wabicon Lake, 135 reciprocal megohms, and of either Mud or Pope Lake of the Waupaca Chain, 240 reciprocal megohms, establish new upper limits to the known range of *Spongilla fragilis* and *S. lacustris* respectively for this factor.

An attempt to collect sponges from the Yahara River basin in the vicinity of Madison proved rather unsuccessful. High winds rendered it impractical to work on the lakes themselves, and examination of the river below Lake Monona, and in the channel and vegetation-choked widespread below Lake Waubesa yielded not a single specimen. Conditions which might explain the absence of sponges include straightening and parking the banks of the river in and near Madison, extensive pollution by commercial fishermen below Lake Waubesa, and the treatment of Lake Monona with copper sulfate to

prevent excessive growth of algae. Above Lake Mendota, the upper Yahara (known as "Catfish Creek") was wide, rather shallow, with little current, and contained a large amount of silt. The channel had been dredged and the marginal vegetation (mostly *Typha*) cut back to permit seining, thus leaving few snags or other suitable attachments for sponges. The few submerged timbers found were covered with silt, however, two sponge colonies were secured from driftwood, both *Heteromyenia repens* Potts, the larger about the diameter of a dime.

The Prairie River, north of the town of Merrill, was similarly poor in sponge fauna. Although the water is clear and inundates a number of large tree buttresses which should form favorable attachment for sponges, only two small colonies were found, both on a floating piece of driftwood. The larger, a colony of *Spongilla fragilis* about 7 mm. in diameter, contained gemmules; the smaller, unidentifiable because of the absence of gemmules, was a delicate colorless film having spined acerate and no dermal spicules. As the floating support of these colonies might easily have entered the river a short distance above the point at which it was examined, this collection furnishes no positive evidence that *S. fragilis* could actually grow in the water of the Prairie River. For that reason, this collection of *Spongilla fragilis* is indicated by an interrogation mark in Table I and figure 1.

In contrast to the vicinity of Madison, the lakes of the Green Bay drainage area furnish excellent opportunity for the study of relatively natural habitats in waters high in calcium and magnesium.

CALCIUM AND THE DISTRIBUTION OF FRESH-WATER SPONGES

Stephens ('20) regarded *Heteromyenia repens* and *Spongilla lacustris* as lime shunning forms. Old ('32) stated that "All Michigan species seem to prefer waters of zero carbonate content." He found *Heteromyenia argyrosperma* limited to waters of low methyl orange alkalinity, and *Tubella pennsylvanica*, *H. repens*, and *H. argyrosperma* all limited to low temporary hardness. Jewell ('35) pointed out correlations between the distribution of the various species of Spongillidae and bound CO₂ and conductivity of the water, and indicated that these correlations might be due to a single factor, since both the conductivity and the bound CO₂ of lake waters are due largely to the carbonates of calcium and magnesium.

Recently the Wisconsin Natural History Survey has made a study of the calcium and magnesium content of lake waters, the results of which have been published by Juday, Birge, and Meloche ('38), and these analyses were made available to the author. By combining the data on distribution in relation to calcium and magnesium content of the waters of the 103 lakes and 15 streams previously studied with the data presented in this paper, two graphs have been prepared to show the frequency of each species of sponge in the various concentrations of calcium and magnesium (Figs. 1 and 2). A few of the waters

from which sponges were collected have not been analyzed for calcium and magnesium, however, to judge from the bound CO_2 content, they would probably not extend the range of any species shown on the graph.

The distribution of species with reference to calcium (Fig. 1) corresponds better with the association of the different species in nature than does the distribution with reference to magnesium (Fig. 2), and, as experimental work

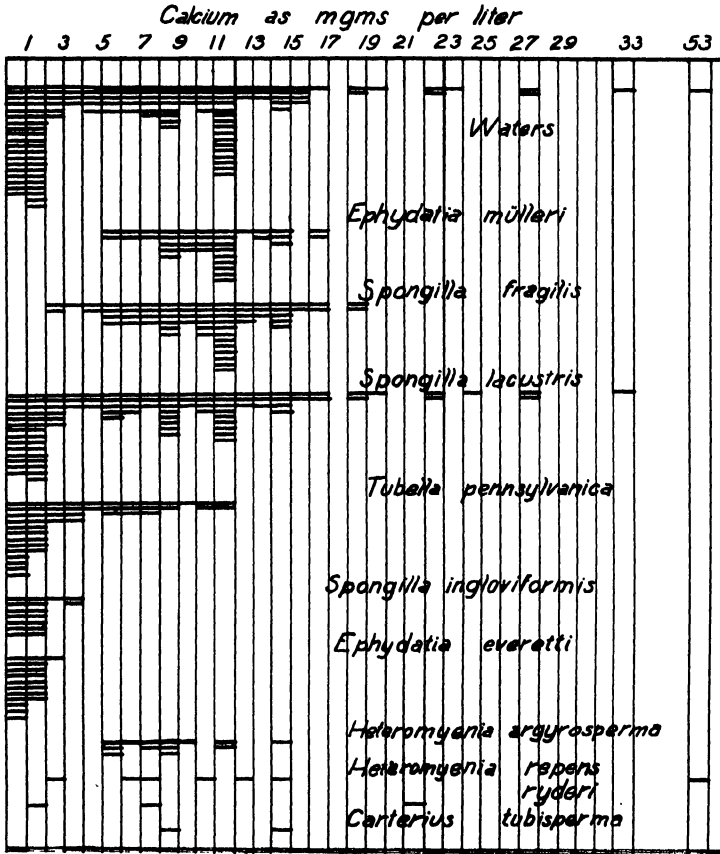


FIG. 1. Graph showing the occurrence of Spongillidae in waters of various calcium concentrations. Vertical lines represent the concentrations of calcium as mgms. per liter. Each horizontal line represents a lake or stream from which sponges were collected. The upper curve shows the frequency of sponge bearing waters of the various concentrations of calcium. The remaining curves show the number of lakes or streams of each calcium content from which each of the nine species of Spongillidae named was collected.

to be mentioned later seems to indicate that calcium rather than magnesium is responsible for the restriction of some species to moderately hard waters and others to very soft waters, it is probable that the apparent correlation between magnesium and sponge distribution shown in the graph is due to the fact that, ordinarily, magnesium and calcium are associated in natural waters.

A study of figure 1 indicates that *Ephydatia mülleri* is restricted by both low and high calcium. It is also significant that, in the water of highest calcium content from which this species was collected (the outlet of Big Lake of the Manitowish, reported in 1935), the collection consisted of a single small colony, and that in Martha Lake, with a closely similar calcium content, the few specimens secured appeared as fragile brownish incrustations. On the

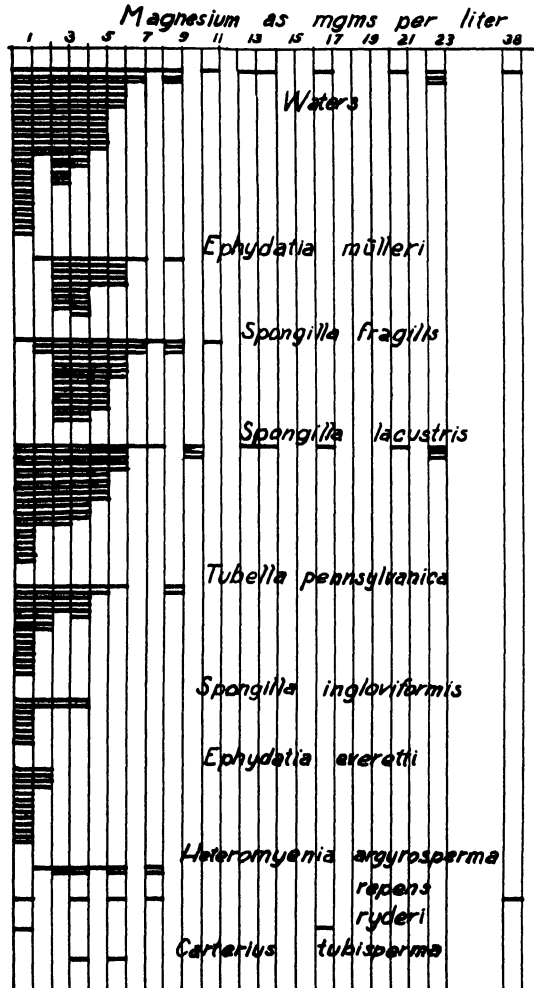


FIG. 2. Graph showing the occurrence of Spongillidae in waters of various magnesium concentrations. Vertical lines represent the concentrations of magnesium as mgms. per liter. Each horizontal line represents a lake or stream from which sponges were collected. The upper curve shows the frequency of sponge bearing waters of the various concentrations of magnesium. The remaining curves show the number of lakes or streams of each magnesium content from which each of the nine species of Spongillidae named was collected.

other hand, the largest, most vigorous, and most abundant colonies of this species were collected from waters of the central and lower part of its calcium range.

Spongilla fragilis is limited by low calcium. As to whether it is also restricted by high calcium in the absence of marl deposition, the data are somewhat inconclusive. If the small colony already mentioned as taken from a floating log in the Prairie River actually grew where it was found, then the range of this species covers practically the entire range of calcium concentrations without marl formation. Colonies of *S. fragilis* growing in waters high in calcium form a thinner more uniform incrustation of much firmer and finer texture than colonies in waters nearer the central and lower part of the calcium range. They are also more commonly brownish in color. These differences were very pronounced in sponges collected from waters having a calcium content of 15 or more mgms. per liter.

Tubella pennsylvanica Potts appears to be definitely limited by calcium. Although collected from waters having a calcium content up to 11.7 mgms. per liter, the colonies secured from such waters were invariably found embedded in the mucky bottom, on decaying wood fragments in a submerged pile of wood debris at the site of an old sawmill, or in some similar environment of rapid organic decomposition. In such an environment it is probable that the calcium in the water would combine with organic acids, and so be rendered innocuous to the sponge.

Spongilla ingloviiformis Potts and *Ephydatia everetti* (Mills) appear to be definitely restricted to waters of a calcium content below 4 mgms. per liter. That calcium is actually the limiting factor in the case of *S. ingloviiformis* but not of *E. everetti* is indicated by experiments to be discussed later. *Heteromyenia argyrosperma* Potts is apparently, like *Ephydatia mülleri*, confined to waters of moderate calcium content, although the number of collections of this species is insufficient to warrant conclusions. Three species, *Spongilla lacustris*, *Heteromyenia repens*, and *Heteromyenia ryderi* Potts, appear to be independent of the calcium content of the water. This is at variance with the findings of Stephens ('20) and of Old ('32) who regarded *Heteromyenia repens* as limited to waters of low hardness. The fact that two waters were found (Emmons Creek and the Yahara river above Lake Mendota) with higher calcium contents than any waters from which *Spongilla lacustris* was collected, can not be regarded as establishing an upper limit to the calcium tolerance of the species, since Emmons Creek, aside from its calcium content, is a type of stream in which neither the author nor Old ('32) have found sponges; a short deep creek of very cold water which enters from large springs; whereas the amount of silt and the dredging activities in the upper Yahara might account for the paucity of sponges there.

In making a detailed study of the Waupaca lakes, some of which have sponge faunas, the author thought to establish definitely the upper limit of calcium tolerance for the species present. The data in Table I show no corre-

lation between the presence or absence of *Spongilla lacustris* and the calcium content of these lakes. Field observations did, however, show a very definite relation between the absence of *Spongilla lacustris* and rapid marl deposition (Birge and Juday, '11, and Juday, '14, discuss causes of marl disposition in these lakes). Figure 3 is a map of the Waupaca Chain 'o Lakes giving the

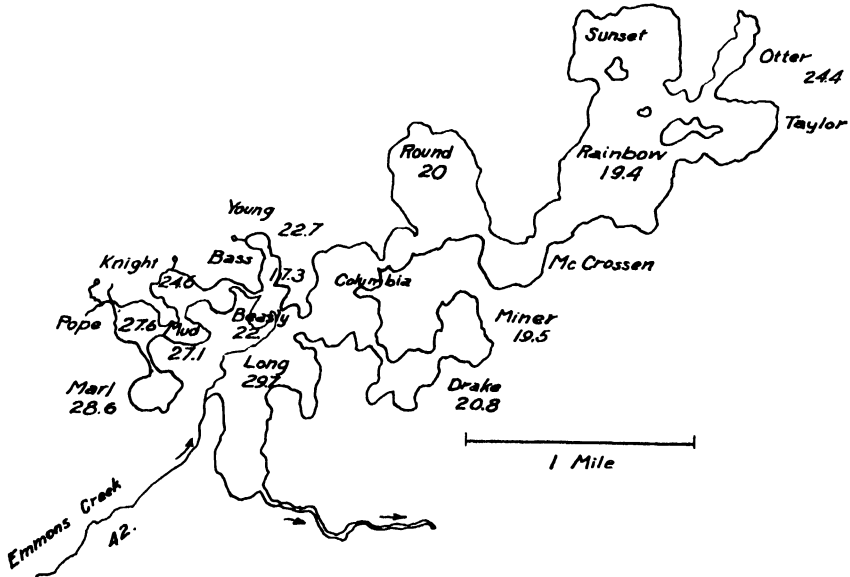


FIG. 3. Map of the Waupaca Chain 'o Lakes giving the calcium content of the water as mgms. per liter. *Spongilla lacustris* was collected from Pope, Mud, Knight, Young, and Beasley Lakes. Marl deposition appeared to be highest in Marl, Rainbow, McCrossen, Round, and the Northeastern part of Columbia Lakes.

calcium content of the water of those from which samples were taken for analysis. The larger lakes of the chain are all depositing marl so rapidly that the bottom, in shallow places, appears to be whitewashed or cemented, and the only submerged vegetation consists in forms, such as *Chara*, which are able to continue apical growth after the older parts are dead and encrusted with lime, giving a peculiar coralline appearance to the sparse bottom flora. The only region where sponges were found was the chain of small lakes at the west end of the group. Of these lakes, Marl Lake, in which no sponges were found, has a gradually sloping margin exposed to the sun. Here the marl deposits are heavy, giving the lake the appearance of a cement basin set in sand. The channel between Marl and Pope Lakes is kept open for the passage of row boats but carries very little water, so that the main source of water in Pope Lake, as also in Mud, Knight, Young, and Beasley Lakes, is a series of springs along the margin. Unlike Marl Lake, these lakes have, for the most part, steeply sloping margins, considerable shade, and black

muck bottoms rich in decaying vegetation. As the water enters from the springs heavily laden with calcium bicarbonate, but without the plankton algae which are responsible for most of the marl formation in the larger lakes, and as CO_2 formed by organic decomposition in the bottom redissolves lime which might otherwise be deposited, the marl deposition is comparatively slow, so that the shallower waters support heavy growths of submerged vegetation on which are numerous colonies of *Spongilla lacustris*. Submerged wood, which in most lakes forms important support for sponge colonies, is here usually barren and lime encrusted. That the organic decomposition of the bottom is an important factor in holding the lime in solution and so favoring sponge life, was further evidenced in the lakes of the upper Oconto and Wolf drainage where sponges were found in bays and lagoons with decomposing muck bottoms, although absent over marl coated bottoms in the same lake.

Probably the transition from spring-fed lake still high in calcium bicarbonate to marl-depositing lake was best shown by Knight Lake. Along the northwestern spring-fed margin submerged vegetation and sponges were abundant, but the shallow, gently sloping, sun exposed bay at the southeast was marl covered and relatively barren. Between these two extremes, a shoal, which extends across the narrow part of the lake exposed to the sun, but subject to more wave action and change of water than the bay, showed considerable marl deposit but, at the same time, supported submerged vegetation and sponges.

Specimens of sponges from the Waupaca Lakes usually show the upper part alive and green whereas the lower part of the same colony may be dead and lime encrusted. This condition is characteristic also of the sponges collected from Chain Lake and the bog near Maiden Lake, and may furnish an explanation as to why *Spongilla lacustris* is apparently the most successful species in surviving conditions of rapid marl deposit. Because of its growth habit, a rapid elongation from numerous apical growing tips, the colony survives long after the original base is dead and lime covered; whereas an encrusting form, such as *Spongilla fragilis*, would soon be marl covered and killed. That the ability of *Spongilla lacustris* to survive marl deposition is due to the rapid elongation of its branches is further evidenced by the fact that, although a large number of specimens collected as late as August 20th, were examined for gemmules, not a single gemmule was found. Ordinarily, in *Spongilla lacustris*, there are no gemmules in the growing "finger tips," but the older basal part of the colony and the lower parts of the "fingers" become packed with gemmules before they die. The fact that there were no gemmules whatever in the lower marl encrusted parts of these Waupaca sponges would indicate that, instead of dying a natural death and then becoming lime covered, they had been killed by the deposition of lime before the completion of their normal life cycle. It is possible that gemmule formation occurs later in the autumn after the activity of marl forming algae has de-

creased, otherwise these sponges must pass the winter in the vegetative form.

The only sponge, other than *Spongilla lacustris*, collected from the Wau-paca Lakes was *Heteromyenia ryderi* Potts. Two colonies of this species, the larger a vigorous looking colony about 5 by 6 by 9 cm., were found on the vegetation near the surface at the head of the outlet of Young Lake on August 4th. Neither colony contained gemmules. However, characteristic birotulate spicules of both types found scattered in the sponge made possible the identification. It is not uncommon in the *Heteromyenias*, and also in *Ephydatia everetti*, to find typical gemmule birotulates in the tissues where no gemmules exist. It may be that these result from a tendency to precocious formation of the gemmule crust, or to the checking of gemmule formation after it has started. Extensive search in the same locality on August 20th failed to reveal any further colonies of this species.

From the field data it then appears that *Spongilla lacustris*, and probably also *Heteromyenia ryderi*, are independent of the calcium bicarbonate content of the water; but that their tolerance for marl deposition depends upon an environment so favorable otherwise as to enable them to grow more rapidly than they are encrusted and killed.

EXPERIMENTAL STUDY

Since previous as well as the present field studies seem to indicate a correlation between the distribution of the various species of sponges and bound CO_2 and conductivity, both of which result largely from calcium bicarbonate, and also with SiO_2 , which is used by the sponge in spicule formation, a series of experiments was undertaken for the purpose of ascertaining the effects of these factors taken separately.

The Forestry Bog, a small bog lake with sphagnum margin located near the Biological Station, was selected as a basic source of water. An analysis of this water shows Free CO_2 , 9.0 mgms. per liter; Bound CO_2 , 1.5; O_2 , 5.35; SiO_2 , 4.1; Ca, 0.9; Mg, 1.84; pH 5.1; Residue, 33.7; Conductivity, 9.5 reciprocal megohms, and color, 70. It is thus a very soft water relatively high in organic content, and with silicon sufficient for spicule formation. As no sponges have been found growing in this bog, danger of introducing sponge fragments with the water was eliminated.

Eleven wooden half kegs of about 25 liters capacity each were set in the sphagnum mat near the margin. A small pump with its intake about two feet below the surface near the centre of the bog was used for securing water. Ten liters of water were added to each tub at least twice daily, and at more frequent intervals in hot weather. An enamel water pail was used in transferring sponges to the experiment and in changing the water. Any chemicals added to the water were thoroughly mixed in the pail before the water was introduced into the experimental tubs. The first and last tubs contained unmodified bog water. The only difference between these two was that No.

11 was a slightly deeper tub than the others used in the experiment, and was placed in a more shaded location than No. 1, and so preserved a lower temperature. Tubs No. 2 and 3 were modified by the addition of $\text{Ca}(\text{HCO}_3)_2$ to establish a bound CO_2 contents comparable to the hardest waters of Vilas County, and the waters of southern Wisconsin respectively. The $\text{Ca}(\text{HCO}_3)_2$ was prepared by making a suspension of lime in water and bubbling CO_2 through it until the cloudiness disappeared. Tub No. 4 was modified by the addition of NaHCO_3 to give a bound CO_2 content equal to that of a hard water but without the calcium. A solution of baking soda was used, and CO_2 bubbled through the water until it reacted acid to phenolphthalein. Tub No. 5 contained 0.145 gms. per liter calcium lactate, which would give the calcium equivalent of a water having 35 mgms. per liter bound CO_2 , but without the CO_2 . Tubs No. 6 and 7 were modified by the addition of sodium silicate to the equivalent of 20 and 40 mgms. per liter SiO_2 respectively. The alkalinity due to the addition of sodium silicate was remedied by bubbling CO_2 through the water. The lower of these two silica contents is approximately the same as the highest silica content found by the author in a sponge bearing water (Wa bi kon Lake, SiO_2 20.5 mgms. per liter). For tubs 8 and 9 a solution was prepared containing 1 part MgSO_4 to 7 parts NaCl , or about the same proportion of these two salts as is found in sea water. It was then determined by trial how much of this solution to add to 10 liters of bog water to give conductivities of 150 and 400 reciprocal megohms; conductivities equal to those of the very hardest waters. Tub No. 10 contained the $\text{Ca}(\text{HCO}_3)_2$, sodium silicate, and salts, in the same amounts as were added to tubs 2, 6, and 8 together.

Except for *Ephydatia mülleri* and *Spongilla fragilis*, which are found only in waters of moderate hardness, the sponges used in the experiment were transferred from very soft water lakes with SiO_2 contents below 0.5 mgms. per liter (Little Rudolph, Weber and Trilby). It was then possible to determine, by microscopic examination, just what parts of the sponge colony developed after the transfer, as the spicules developed in waters of higher silica content are readily distinguished by their greater robustness (Jewell, '35). The sponges used were transferred to the experimental tubs July 23rd, 25th, and 26th. Since two species, *Tubella pennsylvanica* and *Spongilla lacustris*, transferred on the exceedingly hot afternoon of the 25th appeared to have been injured or killed by the transfer, fresh specimens of these were introduced August 1. The experiment was terminated August 23rd. The results of the experiment are given in Table II.

An examination of Table II shows that the addition of NaHCO_3 to a bound CO_2 content approaching that found in Chain Lake or the Waupaca Lakes proved rapidly fatal to all species used in the experiment.

The substitution of calcium lactate for calcium bicarbonate equivalent to the calcium content of a hard water (Tub No. 5) proved fatal to all species except *Spongilla ingloviformis*, a species restricted in nature to waters of

the very lowest calcium content. It is improbable, however, that this result was due to any direct effect of either the calcium or the lactic acid as such, for the high organic content of this water soon induced a heavy growth of bacteria and slimy water moulds which festooned the sides of the tub and every twig or stone introduced as a support for sponges. It is in keeping with the occurrence of *Spongilla ingloviformis* in natural waters of high organic content that it should be the species best able to survive the conditions developed in this experiment. Even this species has never been found in nature in water so rank with bacterial slime and mould. The experiment would indicate that the effect of calcium in restricting the distribution of certain species of sponges in natural waters, is due to its presence in the form of the bicarbonate, and that it is without such effect when in an organic combination.

TABLE II. Table showing the effect upon sponge life of chemically modified waters. An asterisk (*) indicates that the sponge made some slight growth after transfer to the modified water, but was either dead or had decreased in size at the close of the experiment. A check mark (#) indicates that the sponge colony grew visibly and survived the experiment. Blank spaces indicate the colony died without development after transfer.

Duration of experiment, for *E. mülleri* and *S. fragilis*, July 23 to Aug. 23; for *S. ingloviformis* and *E. everetti*, July 26 to Aug. 23; for *S. lacustris* and *T. pennsylvanica*, Aug. 1 to Aug. 23.

Tub No.	Solution	Analysis of water after 12 hours in experimental tubs			<i>E. mülleri</i>	<i>S. fragilis</i>	<i>S. lacustris</i>	<i>T. pennsylvanica</i>	<i>S. ingloviformis</i>	<i>E. everetti</i>
		Bound CO ₂	pH	Conductivity						
1	Bog water control	1.5	5.9	14	#	#	*	*	#	#
2	Ca(HCO ₃) ₂ to 20 mgms. per l. Bound CO ₂	25.0	7.7	93	#	#	*	*	#	#
3	Ca(HCO ₃) ₂ to 40 mgms. per l. Bound CO ₂	39.0	8.0	140		*	*			*
4	NaHCO ₃ to 40 mgms. per l. Bound CO ₂	47.0	7.8	178						
5	Calcium lactate to Ca equivalent of No. 3	12.5	6.7	87					*	*
6	Sodium silicate to 20 mgms. per l. SiO ₂ ..	5.0	6.5	25			#	*	*	#
7	Sodium silicate to 40 mgms. per l. SiO ₂ ..	12.0	6.8	48			*	*	*	*
8	MgSO ₄ and NaCl to Conductivity of 150	1.5	5.8	150				*	#	#
9	MgSO ₄ and NaCl to Conductivity of 400	1.5	5.6	400				*	*	*
10	Ca(HCO ₃) ₂ as in No. 2 Sodium silicate as in No. 6	28.0	7.6	240	#	*	#	*	#	#
11	MgSO ₄ and NaCl as in No. 8 Bog water control	1.5	5.9	14	#	*	*	*	#	#

Concerning the experiments which more nearly duplicate natural conditions, *Ephydatia mülleri* and *Spongilla fragilis* survived only in waters to which some calcium bicarbonate had been added. Even in these waters, *Ephydatia mülleri* died in the higher concentration. These results are in keeping with the known distribution of these two species in nature (Fig. 1).

Spongilla ingloviformis failed to survive in any of the waters to which calcium bicarbonate had been added or in the higher concentration of sodium silicate, a result again in keeping with the restriction of this species in nature to soft acid waters, and with the fact that it has never been found coexistent with either *Spongilla fragilis* or *Ephydatia mülleri*.

Tubella pennsylvanica made a weak growth in water containing calcium bicarbonate equivalent to 25 mgms. per liter bound CO_2 , as shown by microscopic examination of the spicules, although the colony was dead and largely disintegrated by the close of the experiment. No growth whatever was made in the higher concentrations of calcium bicarbonate or of sodium silicate, although growth was apparently unaffected by the addition of magnesium sulfate and sodium chloride to a conductivity more than double any in which this species has been found in nature. This would seem to confirm that, although less sensitive than *Spongilla ingloviformis*, *Tubella pennsylvanica* is restricted by the calcium bicarbonate content of many moderately hard to hard waters.

Spongilla lacustris, in these experiments as in the field, appears to be relatively independent of the calcium content of the water. Its failure to survive in both waters to which magnesium sulfate and sodium chloride were added can not be attributed directly to conductivity, since it survived in Tub No. 10 in a conductivity of 240 reciprocal megohms, and has been found in nature in waters similarly high in conductivity.

The survival, in tubs 8 and 9, of the three species not found in nature in waters of high conductivity, would indicate again that calcium bicarbonate, rather than the conductivity of the water, is the limiting factor in their distribution.

Although experiments 8 and 9 were originally planned to test the effects of conductivity apart from the effects of calcium, the results are of interest also in that these waters furnish a moderately high magnesium content associated with low calcium. The magnesium added, as MgSO_4 , to tubs 8 and 9, amounted to 1.66 and 5 mgms. per liter respectively. This, in addition to the 1.84 mgms. already present in the bog water, gave magnesium contents of 3.5 and 6.84 mgms. in a water containing only 0.9 mgms. per liter calcium. Reference to figures 1 and 2 shows that comparable magnesium contents of natural waters are associated with the presence of *Ephydatia mülleri* and *Spongilla fragilis* and the restriction or complete absence of *Spongilla ingloviformis* and *Ephydatia everetti*, whereas comparable calcium concentrations are associated with the absence of *Ephydatia mülleri* and *Spongilla fragilis*, although favorable to *Spongilla ingloviformis* and *Ephydatia everetti*. Since, in the experiment, the two hard water species perished while the soft water species survived, the results tend to confirm the opinion already stated on the basis of field observation, that calcium, rather than magnesium, is responsible for the restriction of some of the species studied to soft waters and of others to waters of moderate hardness; and that the apparent correlation between magnesium and sponge distribution shown in Fig. 2 is due to the fact that magnesium is usually associated with calcium in natural waters. Although it is possible that magnesium in the form of the bicarbonate might supplement the effects of calcium bicarbonate, the indications are that magnesium in the form of the sulfate (the form in which it most

commonly occurs in nature) has no effect upon the distribution of the species of sponges studied, in the concentrations in which it ordinarily occurs.

Ephydatia everetti alone, of the six species used in the experiments, gave results wholly unpredictable on the basis of its known occurrence in nature. All of the twenty-four lakes from which the author has collected this species are seepage lakes of the extremely soft water type, showing a variation in bound CO_2 of 0.5 to 4.5 mgms. per liter, pH 5.0 to 6.6, SiO_2 0.0 to 0.8 mgms. per liter, and conductivity 7.5 to 19.0 reciprocal megohms; yet this same species made a profuse growth, spreading onto adjacent twigs and leaves, in water with a bound CO_2 content more than five times that of any water from which it had been collected, in a water with a silicon content over twenty times that of its natural environment, and in water with a conductivity twelve times that of any water from which it has been collected. *Ephydatia everetti* has also made good growth in unmodified water from Trout Lake, a drainage lake having 11.2 mgms. per liter calcium. It is evident, therefore, that the restriction of this species to seepage lakes of the extremely soft water type can not be the direct result of the chemical content of the water.

SUMMARY

1. Fresh-water sponges have been collected from waters varying in calcium content between 0.3 and 53.4 mgms. per liter, and in magnesium contents varying between 0.0 and 38 mgms. per liter.

2. The distribution of the various species of Spongillidae studied is affected by calcium rather than by magnesium. The effects of calcium in limiting the distribution of sponges are due to its presence in the form of calcium bicarbonate. Calcium present in organic combination has not the same effect.

3. Apparent correlations between sponge distribution and conductivity, bound CO_2 , and magnesium, are due to the dependence on, or correlation of, these factors with the calcium bicarbonate content of most of the natural waters in the area studied.

4. *Ephydatia mülleri* is absent from both high and low calcium waters. It has been taken from waters varying between 5.6 and 16.3 mgms. Ca per liter, but shows the most vigorous growth in waters of the central and lower parts of its range.

5. *Spongilla fragilis*, although less selective, is similarly limited by low calcium concentrations and probably also by high concentrations. It has been found growing in waters varying between 2.08 and 18.6 mgms. per liter calcium.

6. *Heteromyenia argyrosperma* has been collected from waters varying from 5.45 to 14.4 mgms. per liter calcium. It is probably restricted to waters of moderate hardness, although further collections are needed.

7. *Tubella pennsylvanica* has been collected from waters varying from 0.3 to 11.8 mgms. per liter calcium, although much more abundant and

luxuriant in waters at the lower end of its range. When found in waters having a calcium content over 6 mgms. per liter it has always been in a location of rapid organic decomposition—a condition which might well reduce the calcium bicarbonate content of the water in the immediate vicinity of the sponge.

8. *Spongilla ingloviformis* is the most calcium sensitive species yet found. It has not been taken from waters having a calcium content over 3.16 mgms. per liter, although common in waters of lower calcium content.

9. *Ephydatia everetti*, like *Spongilla ingloviformis*, has been collected only from waters of extremely low calcium content (2.5 mgms. per liter and less). Unlike *Spongilla ingloviformis*, however, this species is able to grow and form gemmules after transfer to waters of much higher calcium content than any from which it has been collected.

10. *Heteromyenia repens* and *Heteromyenia ryderi* are both tolerant of a wide range of calcium content. The former has been found in waters varying from 2.66 to 53.4 mgms. per liter, and the latter in waters varying from 1.2 to 22 mgms. per liter. Both species thus appear to tolerate practically the entire range of calcium content found in Wisconsin waters.

11. *Spongilla lacustris* appears unaffected by the calcium content of the water as it has been found growing luxuriantly in waters varying from 0.16 to 32.4 mgms. per liter. It is, moreover, able to survive in waters where lime is being deposited in the form of marl. This ability appears to be due to the rapid rate of growth and the growth habits of the colonies. Under otherwise favorable conditions, the sponge colony can grow upward from the tips of its numerous finger-like branches more rapidly than the depositing marl encrusts and kills it.

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MICROCLIMATE AND A NOTABLE CASE OF ITS INFLUENCE ON A RIDGE IN CENTRAL INDIANA

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The term microclimate or habitat climate has become well established in European literature but American workers have used it very sparingly. Microclimate refers to the finer modifications of the macroclimate or climate in the broader sense in which it is used in meteorology. While vegetation in its gross aspects is determined by the macroclimate, the microclimate is the real plant climate and plant association determiner, for the very presence of plants means modification of the purely gross meteorological climate conditions.

Geiger ('30) says, "That microclimate differs greatly from the records of the weather station reports has been known for a long time, as for instance the variation in the occurrence of frost within the narrow confines of a certain locality, but how great and extensive these divergencies may be in this special climate near the earth's surface has been discovered only recently through numerous measurements, and there are without doubt, still many surprises in store for us, for the moisture relationships have hardly been touched in a microclimatic way." He sums up the problems by saying, "The goal of the investigation in microclimatology must be to attempt to discover the physical laws which govern the deviations of the microclimate from the macroclimate. Microclimatology will give us a better understanding of atmospheric happenings." He believes that in densely populated areas it is almost more important to know the existing microclimatic variations than those of the generalized macroclimate. These variations are certainly important in the analysis of minor and at times of major differences in vegetation types, and in forestry and agricultural experiments, and here in Indiana in solving of the soil erosion problem.

Many variations in microclimate are due to topographic differences, as Cowles ('01) has shown, but microclimate involves more than mere variation in topography. Of importance also are structure, color, aeration and water-holding capacity of soil, reaction of plant cover on the habitat, differences in erosion and run-off. One must also include not easily defined variations in temperature and precipitation in regions with apparently small physiographic and topographic variations which Visser ('36) has described for Indiana.

Indiana as a whole is a rather uniform plain, yet its climate is not so uniform, even in the same latitude, as is usually assumed. Visser ('36, '37).

points out that variations in microclimate are evident even from records of rather widely scattered weather stations. The interesting feature of his maps is that variations in climatic expression are found within comparatively narrow confines of a region and one can not point to a topographic variation as cause of them. Here, then, we have greater differences in microclimate which experience more and more modification, shading into finer gradations in the lower strata of the vegetation cover as shown by Wilson ('36) in her work on epiphytic mosses.

The macroclimate is extensive and more or less uniform in its cycles. The microclimate is complex, frequently very limited in extent, exerts local control and imposes modification on the expression of the macroclimate. The macroclimate finds expression in the large plant communities, the more or less homogeneous formations of Weaver and Clements ('38). Microclimate primarily makes formations heterogeneous and breaks the larger units up into vegetation or forest types, the associations, associates; consociations, consocieties; societies and socies of the above authors. It also makes it possible for smaller groups of preclimax vegetation to persist at relict colonies long after macroclimatic changes have shifted formations. Friesner and Potzger ('35) found that relict colonies of hemlock in Indiana grow in circumscribed areas where evaporation is higher and soil moisture less than in adjacent areas of deciduous forest.

Many errors have been made in descriptions of forest cover types in areas of the deciduous forest because the workers evidently assumed a uniform macroclimatic control. As Friesner ('37) has shown, Indiana is a critical botanical area where prairie and boreal vegetations extend into the deciduous forest, indicating local persistence of these climatic belts as microclimatic controls, and where oak-hickory and beech-maple struggle for dominance over crown cover.

Even when the sharp controls of differences in forest types are recognized, the differences in plant climate cannot be appreciated fully without quantitative field data. The influence of slope and elevation on vegetation has been appreciated more fully in areas of the eastern deciduous forest where elevation is greater than in Indiana. Thus, Braun ('35) has shown a definite control by slope and exposure of the plant communities on Pine Mountain in Kentucky. Cain ('31) investigated acidity of soil in relation to differences in slope and the changes in plant communities associated with it in the Great Smoky Mountains. In most instances the workers have made no attempt to correlate habitat factors quantitatively with plant distribution but merely described the topography and the corresponding change in vegetation.

The United States Department of Agriculture selected Indiana for a special study in erosion because it is thought that this state is representative of a large area in the Midwest. In this study Visser ('37) found that in many instances differences in erosion were frequently caused by small local variations in the topography, which at times were not even apparent. The

same author also shows that erosion is frequently correlated with specific types of natural vegetation. We might, thus, be justified in assuming that the present soil moisture and evaporation studies are representative of wide areas of the eastern deciduous forest, which like Indiana, have small physiographic variations.

In the dissected driftless area of Indiana we have striking differences in forest types. Thus, the author ('35) pointed out that in Monroe County south¹ slopes supported primarily oak-hickory and north slopes beech-maple forest types. The division between these two types is so sharp that one might walk along the sharp ridges and touch both types of forest. The present study was an attempt to investigate the real differences in some of the habitat factors on the two slopes. Evaporation and soil moisture variations were studied over a period of twenty weeks during the summer of 1934 on one typical ridge and the vegetation was correlated with differences in slope.

GEOGRAPHIC AND PHYSIOGRAPHIC FEATURES

The ridge selected for observation was in Salt Creek Township, Monroe County, Indiana, in the same locality where the study of 1931-32 was carried out. The whole region is much dissected and the numerous valleys tributary to the master valley give rise to a series of steep ridges. These ridges are forest covered but differ in forest type with exposure. The ridge studied was comparatively uniform as to its two slopes, the north slope being 505 feet and the south slope 539 feet from valley floor to ridge top. On both slopes the crowns of the trees formed a closed canopy.

METHODS

Four Livingston porous bulb atmometers were placed at 130-foot intervals on each slope and one on the ridge top. Unfortunately the ridge top was the lane for hunters and farmers passing through and the atmometer had to be concealed somewhat, and so in all probability does not record the severest and typical ridge-top evaporation.

Atmometer readings and soil samples at surface and six-inch levels were taken once a week for a period of twenty weeks from May 20 to September 30, 1934. The soil was placed into tin boxes with tight-fitting lids. In order to save the weekly trip of approximately 130 miles, Mr. Willie Souder, a resident of Moores Creek valley, made the readings and collected the soil. The cans were packed tightly and mailed to Indianapolis. Readings were always made on the day of their arrival. The time in transit was about the same for each week's collection. Five closed cans weighed at three-day intervals showed the negligible loss of only .05 to .08 grams. Percentage of moisture was computed on dry weight of the soil.

¹ The designations south and north slopes are always used in the sense of south-facing and north-facing slopes.

DISCUSSION

It is a well recognized fact that climate has its expression in vegetation and for the greater part of Indiana this vegetation is the deciduous forest. The component species of this formation vary greatly in their potentiality for adjustment to environmental conditions. Some are limited to an optimum mesophytic habitat while others can endure habitats which border on xerophytism. As Warming ('09) aptly points out, "Some deciduous trees, for example *Quercus*, are comparatively xerophytic, while others are decidedly mesophytic, as *Fagus* and *Acer*." This diversity is clearly expressed in the many forest types which foresters have adopted for the eastern part of the United States ('32). Lately Friesner ('37) pointed out that Indiana is the "crossroads" for numerous species, and so the microclimate exerts a major influence even on forest types, which may be along such sharp-cut lines as in

TABLE I. Line transect from foot of north-facing slope to foot of south-facing slope. Distribution of species, total number of stems.

Species	Quads. 1-5	Quads. 6-8	Quads. 9-11	Total stems N-fac- ing	Ridge	Quads. 13-18	Quads. 19-23	Total stems S-fac- ing	Grand total
<i>Acer saccharum</i>	a ¹ 12	79	91	182		14	5	19	N S
	b 2	3	9	14		7	2	9	
	c	6		6		2	1	3	
<i>Fagus grandifolia</i>	a 2	3	1	6					202 31
	b 2	1	—	3					
	c 3	3	2	8					17 —
<i>Carpinus caroliniana</i>	a 92		1	93					
	b 19			19					
	c								112 —
<i>Juglans nigra</i>	a 1			1					
	b —			—					
	c 3			3					4 —
<i>Liriodendron tulipifera</i>	a 1			1					
	b —			—					
	c 7			7					8 —
<i>Ulmus fulva</i>	a 29	6	3	38					
	b 4	—	—	4					
	c 2	—	—	2					44 —
<i>Carya cordiformis</i>	a 2		1	3					
	b —		—	—					
	c —		—	—					3 —
<i>Carya glabra</i>	a		2	2	4	8	9	17	
	b		1	1	1	8	10	18	
	c		1	1	—	6	3	9	4 44
<i>Quercus alba</i>	a				6	23	2	25	
	b				—	19	17	36	
	c				4	9	10	19	— 80
<i>Quercus borealis maxima</i>	a —	—	—	—					
	b —	—	—	—					
	c 1	1	1	3					3 —
<i>Quercus velutina</i>	a				6	17	2	19	
	b				—	19	17	36	
	c				4	5	10	15	— 70

¹ a represents stems below 1 in. D.B.H. at least 3 ft. in height; b stems 1-5 in. D.B.H., and c stems above 5 in. D.B.H.

the uplands of Monroe County where a ridge top path may skirt beech-maple on one side and oak-hickory on the other (table I).

Microclimate is again, a complex of varying degrees which range from a very sensitive difference to a gradual merging with the macroclimate. Gams ('32) in Europe and Wilson ('36) and Young ('38) in Indiana found distribution of epiphytic mosses controlled by very fine variations in the microclimate as determined by north and south sides of trees, or by differences in elevation of a few feet up or down a slope.

Again, in its coarser aspect, the microclimate may vary vegetations of two climax formations along lines of stress between two macroclimates. Costello ('31) found along the Iowa-Missouri state line that bluffs along the Missouri River were treeless (prairie) on west slopes and densely forested on east slopes. He states that west slopes give the appearance of being almost entirely devoid of trees, and he attributes this to greater evaporation on west slopes due to prevailing winds. Fuller ('12) studied a beech forest near Chicago and found striking differences in evaporation induced by rather small variations in topography, such as shallow ravines, which found expression in a greater abundance of delicate herbs. These physical features of the environment usually induce differences in evaporation, and Livingston ('08) is of the opinion that "The evaporation power of the air is a controlling factor in the determination of the plant population of any habitat."

One could continue to cite many authors who stress a single or several environmental factors which exerted local control on vegetation types, but suffice it to add one more from our western mountain region because the slopes involved were about of the same dimensions as those considered in the present Indiana study. Bates ('33) found a sharp zonation between western yellow pine, Engelman spruce and Douglas fir, controlled by exposure of slope. This author found that soil moisture, evaporation and temperature follow the contour of the slopes closely, with the highest temperatures, water evaporation, and the least soil moisture on the south slopes.

Table II of the present study clearly pictures the sharp zonation between oak-hickory and beech-maple forest in Monroe County. There is no mistaking the sharp control. The more mesophytic beech, maple, and tulip poplar occupy the north and the more xerophytic oaks and hickories the south slopes.

TABLE II. *Tabulation of ten quadrats along the ridge top, each ten meters square.*

Species	Below one inch D.B.H.	1-5 inches D.B.H.	Above 5 inches D.B.H.	Total stems
<i>Carya glabra</i>	7	113	4	124
<i>Carya ovata</i>	—	30	1	31
<i>Quercus alba</i>	2	13	7	22
<i>Quercus velutina</i>	—	10	6	16
<i>Rhus copallina</i>	—	11	—	11
<i>Sassafras variifolium</i>	13	17	1	31

The north slope is also marked by greater abundance of tree species involved in the crown cover (table I).

The north slope stations, except for a few weeks, record the least loss of water. Station "A" at the foot of the slope might have been influenced by air currents along the floor of the trough which induced greater evaporation there than in the atmometer at Station "B" a little farther up the north slope.

The protected position of the atmometer on the ridge top evidently caused somewhat lower water loss than that recorded by the two atmometers farther down on the south slope. The total loss for the season for the four atmometers on the north slope was 5,667.1 cc. and for the four atmometers on the south slope 9,104.1 cc., a difference of 61 per cent (fig. 4, c). These figures assume significance only if translated into edaphic factors or stresses in the water "household" of the plants. For this purpose, available water in soil at surface and six-inch levels was studied week by week and results are presented graphically in figures 1 and 2.

On the north slope, Station "D" is most consistent with greatest soil moisture. This station was in a slight depression in the general sweep of the slope and so apparently retained more of the run-off from the ridge, thus, again, indicating the finer control by the microclimate.

As a whole, surface soil had a higher moisture content than that at six inches depth. For sixteen weeks the north slope stations recorded 30 per cent or more soil moisture while south slope stations had a comparable water content only on four readings. As has been pointed out the summer of 1934 had abundant rainfall in Monroe County, and yet south slope stations dropped below the wilting coefficient on four weeks, but this happened only once on the north slope.

Soil at six-inch depths (fig. 1) is marked by absence of erratic sudden changes, and soil moisture is uniformly lower than in the surface soil. Soil moisture on the south slope dropped below the wilting coefficient on seven occasions but only four times on the north slope. If so many weeks of critical soil moisture conditions occur during a summer with an inch of rainfall a week, one can readily picture the stress during seasons with scant rainfall. The comparative differences between the two slopes in evaporation and soil moisture are shown graphically in figures 1 to 4. Comparing weekly averages, the surface soil has 30 per cent and soil at six inches 28 per cent more moisture on the north than on the south slope.

Now, what climatic features are probably differentially influenced on the two slopes to induce the big differences in the end results? There is first of all the wind: During spring and summer it is primarily from the southwest and south which would accelerate evaporation on the south slope, especially during the early part of the growing season. Secondly, there is more insolation on the south slope which would induce higher temperatures on that slope. Bates ('33) records temperatures up to 60° F. higher on south than north-facing slopes. Even small differences in moisture will produce a cumulative

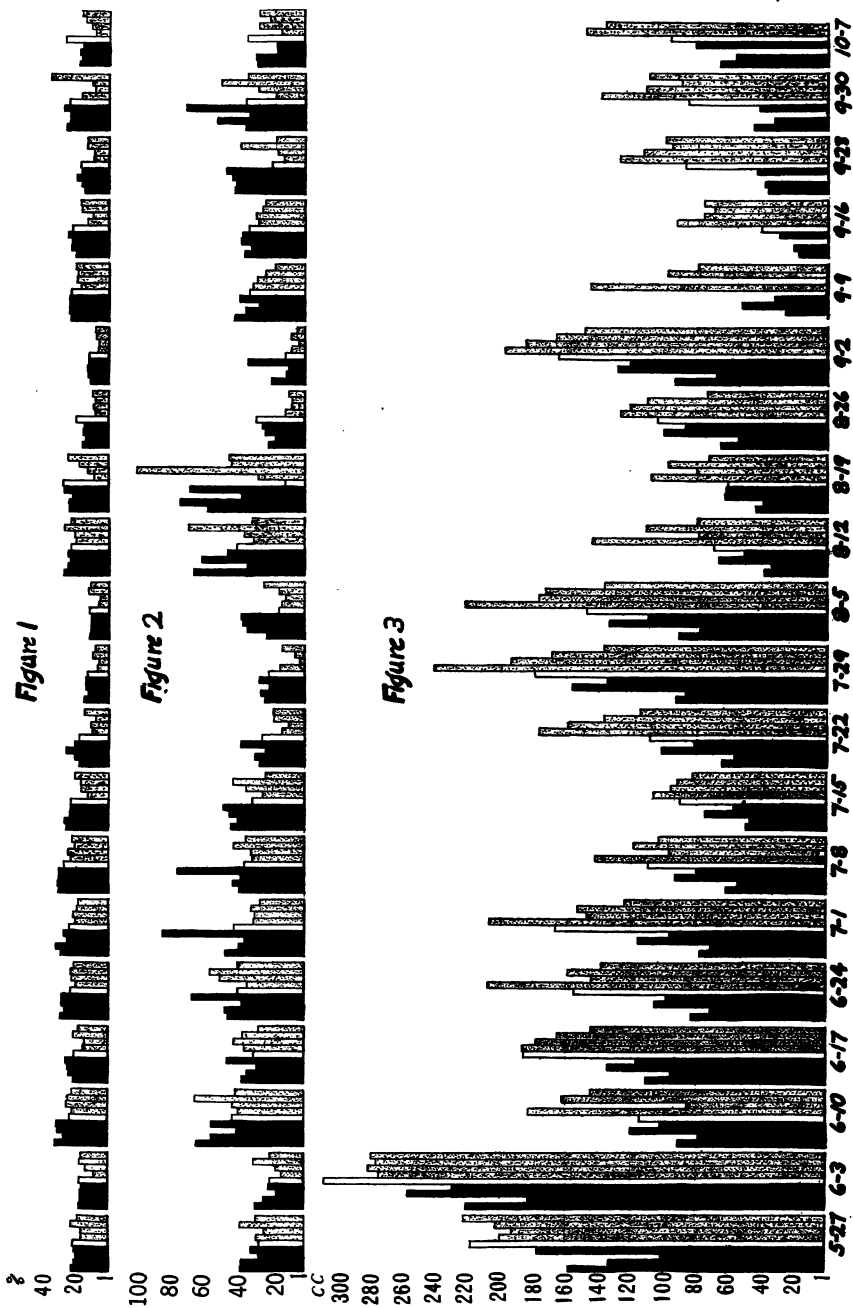


FIG. 1. Percentage of soil moisture at six inches depth.

FIG. 2. Percentage of soil moisture at the surface.

FIG. 3. Weekly evaporation in cubic centimeters. Black columns represent the four stations north slope; stippled those on the south slope; and white that on the ridge.

effect on the habitat as such, which is evidenced by deeper humus on north slopes, this, of course, retards run-off and retains moisture more efficiently.

The sum total of such microclimatic differences finds expression in sharply-delimited different forest types, viz. oak-hickory on the more xeric south slopes and beech-maple on the mesic north slopes (table I).

Results obtained in this study are apparently representative of the control maintaining a dual type of forest on all dissected areas in Monroe and adjacent counties. Friesner and Potzger ('37) show this to be true for Brown and Bartholomew Counties.

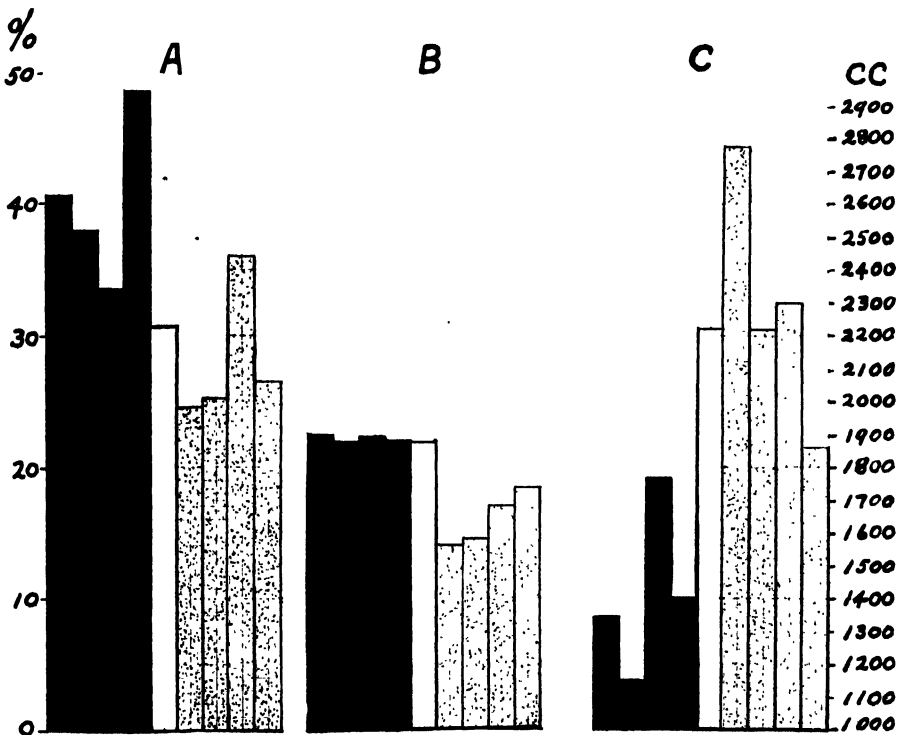


FIG. 4. Average soil moisture for the period of twenty weeks, at the surface (A), and at six inches depth (B). Total water loss by evaporation for the season (C). Black columns represent the stations on the north slope; stippled those on the south slope; and white that on the ridge.

Now, how long will such microclimatic conditions exert major control on this central Indiana area? Physiographically, the whole region is mature, the ridges are about as sharp as they will ever be, the slopes are more or less at their angle of repose, and so physiographic changes will be slow. The microclimate is, thus, more or less a constant cycle which will control these two forest types as long as the macroclimate experiences no change.

SUMMARY

The term microclimate is defined and the opinion expressed that it is most descriptive of local climatic variations.

Ridges in Monroe County, Indiana have characteristically beech-maple forests on north slopes and oak-hickory on south slopes. One of these ridges was studied for a period of twenty weeks as to evaporation and soil moisture differences on the two slopes.

Evaporation was consistently higher on south than on north slopes. For the season 1934, the south slope had 61 per cent more evaporation loss than the north slope.

Surface soil had 30 per cent, and soil at six inches depth 28 per cent more moisture on the north than on the south slope.

Differences in wind, insolation, temperature and humus-content of the soil are suggested as causes for differences in available soil moisture.

The area is physiographically mature with slopes and ridges about at equilibrium, and so little change is likely to occur from the present microclimatic control in this part of Indiana.

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VERTICAL DISTRIBUTION OF SUMMER TEMPERATURE IN THE FALSE BOTTOMS OF CERTAIN MICHIGAN BOG LAKES ¹

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The general features of false bottoms in bog lakes have been discussed by the writer in other publications (Welch, '35, '36a). So common are they, in one form or another, that they are regarded as one of the several features which distinguish bog lakes from other kinds of lakes. Little work has yet been done on the limnological relations of these nebulous transitions from clear water to well-grounded bottom deposits, but certain important conditions which modify the biological production in such lakes are now known, as for example, the presence of a well-developed false bottom eliminates most or all of the macroscopic bottom-dwelling organisms. Absence of a macroscopic bottom fauna is a serious deficiency for any lake and inevitably results in restricted productivity. In another paper, the writer (Welch, '38a) has discussed the relation of false bottoms to the problems of circulation and stratification in bog lakes—problems which involve, among other things, the vertical distribution of temperature. In order to secure a better understanding of this temperature distribution as it occurs in false bottoms in mid-summer, the work on which this paper is based was undertaken.

A thermophone was used as the instrument for measuring temperature. On the smaller "sphagnum" bog lakes, a boat was held securely on the selected spot by long ropes radiating from the boat to trees on the mat; on the larger lakes where the work was done remote from shore, the boat was immobilized by radially arranged anchors. In the former set-up, the thermophone galvanometer was located on shore and the cable sent out to the boat; in the latter, it was necessary to have the whole equipment in the boat. After the boat was located over the selected station, the coil (terminal) of the thermophone was carefully lashed to the end of a sectional $\frac{3}{8}$ th inch iron rod in such a way that it would not be injured when pushed into the firmer, deeper layers of the false bottom. The thermophone cable was lashed to the rod from place to place as the latter was lowered. New sections of the rod were added when needed. This rod enabled the operator to push the thermophone

¹ Contribution from the Biological Station and from the Department of Zoology, University of Michigan.

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coil in a vertical direction and also to sink it to the various desired levels. Temperature readings were taken at frequent and uniform vertical intervals, usually at 0.3 meter. The coil was pushed as deep into the bottom as the safety of the instrument would permit, such a level being regarded as within the true bottom and below the false bottom. Readings were always taken from the lake surface downward. Usually three or four persons were necessary to operate this method so that all of the necessary precautions could be observed.

This work was done in that region in which the University of Michigan Biological Station is roughly the center. This area has many lakes of varying sizes and kinds, among which are numerous bog lakes of diverse types. Eight bog lakes were originally selected as possibly suitable for this kind of investigation. These are known locally under the following names: Bryants, East, Livingstone, Maloney, Mud, Munro, Penny, and Vincent. Three of these lakes—East, Maloney, Penny—were found to have false bottoms so thin that they are not favorable for this type of work and no further attention was given them. All records were made during mid-summer.

All graphs which appear in this paper are drawn to the same scale. The heavy, short, transverse bar across each curve represents the uppermost surface of the false bottom. Figures at the lower end of each curve indicate the temperature values at the deepest point reached by the thermophone coil.

BRYANT'S BOG LAKE

Bryant's Bog Lake has already been described by Coburn, Dean, and Grant ('33), Welch ('36*b*), and others; hence it will suffice here to merely state that it is a small bog lake of the so-called sphagnum type; is completely surrounded by extensive mat formation and peat deposits; is so thoroughly protected by closely surrounding forests and hills that wind action never produces any surface disturbance other than a very minor one; and has peat deposits under the lake which extend to a depth of about 15 meters. The small size of the open water of the lake (area about 430 square meters), the almost complete absence of wave action, and the considerable depth of false bottom made this lake very favorable for the study of heat distribution in a situation in which wind plays virtually no part. The data are expressed in the curves shown in figure 1.

The curve for July 23, 1935, extends only to 3 meters depth since the series of data on which it is based was primarily exploratory and the sectional rod available at that time for lowering the thermophone coil was only 3 meters long. Hence it fails to show the characteristic form of the curves exemplified in the other series. The peculiar form of the curve above the false bottom was doubtless due to the fact that the maximum air temperatures for the previous six days had risen to 30.6–35.0° C., while the minimum temperatures for the same period were 15–20.5° C. Also it should be noted that the read-

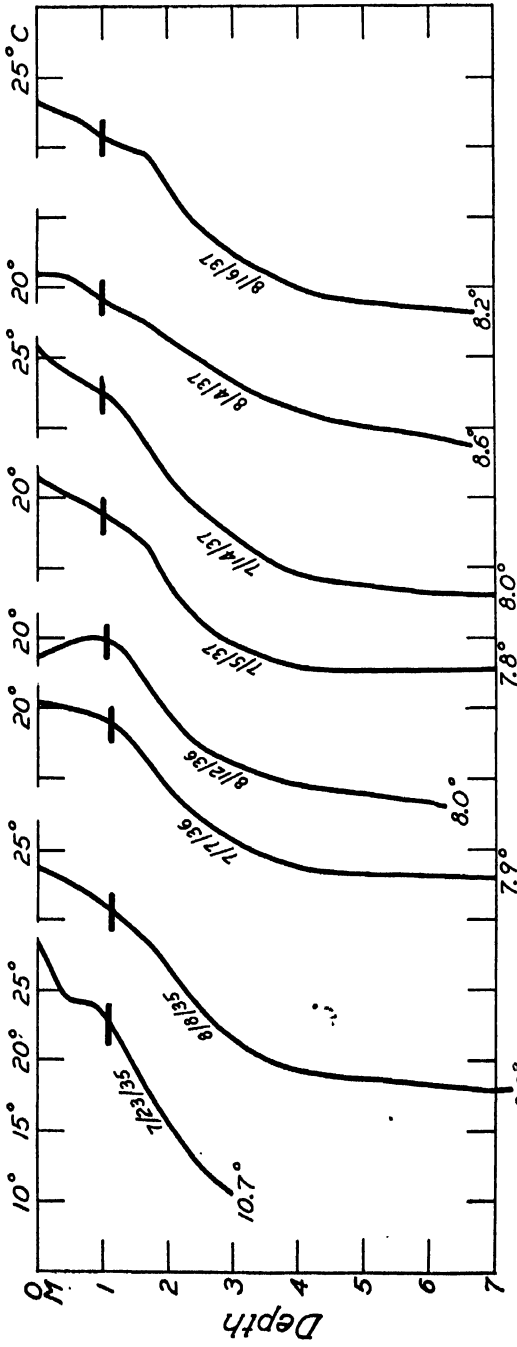


Fig. 1. Curves representing the vertical distribution of temperatures in the false bottom of Bryant's Bog Lake during the summers of 1935, 1936, and 1937.

ings for this curve were taken at 2:00–3:30 P.M. on a day when the maximum temperature was 30.5° C. Persistent high day temperatures had warmed up the surface water layer, but in the absence of wind action the heat transfer was largely by conduction and only the upper part of the temperature curve was changed from the preexisting form.

The top portion of the curve for Aug. 12, 1936, based upon the temperatures of the water above the false bottom, represents a swing in the other direction. This series of records was taken in the forenoon following a night during which the air temperature dropped to 11° C. from a previous minimum air temperature of about 15–16° and from a previous day (Aug. 11) maximum air temperature of 27.7° C. It shows the interesting circumstance of colder, heavier surface water superimposed upon warmer lighter water, due without doubt to the cool preceding night and the lag of readjustment by convection.

The curve for Aug. 4, 1937, seems at first sight to show a distinctly straighter form than those for July 5 and Aug. 16 of the same summer. However, the essential form of the curve has been altered but little since if the upper part of the curve to a depth of about 3 m. is swung over so that the top is at about 26 degrees then the curve would have a shape very similar to that of the curve for July 14. Apparently, previous cooling of the uppermost water had had the effect of straightening the curve.

A comparison of all of the curves indicates a general similarity of form in all of them. Variations in the upper parts of the curves reflect the sequence of changes in air temperatures. The regions most affected by changes of air temperatures are those above the top of the false bottom although somewhat deeper effects are occasionally evident. It will be noted that the top of the false bottom remained at about the same level for the three summers covered by the records.

LIVINGSTONE'S BOG LAKE

Livingstone's Bog Lake is almost a duplicate of Bryant's Bog Lake. The bog is the same type, the materials which compose the false bottom are essentially the same, and the degree of capture of the open water by the encroaching marginal mat is similar. Likewise, the protection against wind action is just as complete. This lake was selected because it offered an opportunity to compare results from two lakes—Bryant's and Livingstone's—which are so strikingly alike.

The curves in figure 2 require little discussion. The distinct bend in the upper part of the curve for Aug. 16, 1937, is due to the effect of high air temperatures of the previous day (about 34° C.). No explanation can be offered at this time to account for the peculiar sharp bend at the lower end of the curve for July 23, or the low temperature encountered at the bottom. This peculiarity was recognized at the time the records were taken and there was no reason for believing that an error was made. The top of the false

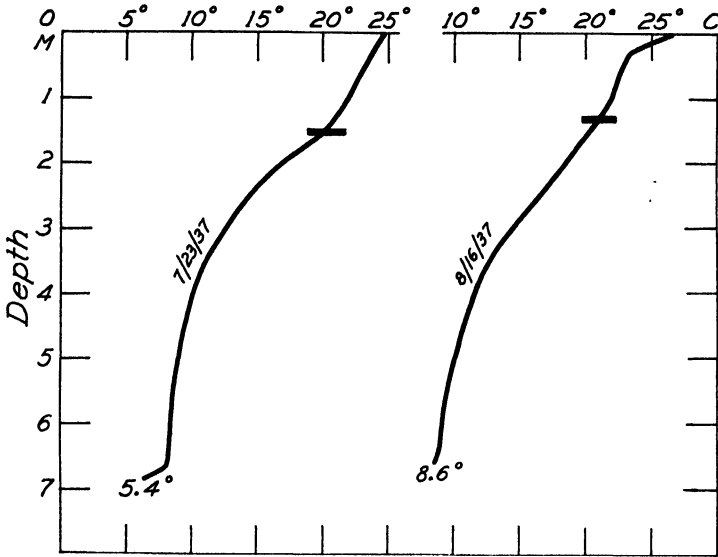


FIG. 2. Curves representing the distribution of temperatures in the false bottom of Livingstone's Bog Lake, summer of 1937.

bottom was somewhat closer to the water surface in later summer. In most essential respects, the vertical distribution of temperature in this lake is similar to that in Bryant's Bog Lake which it resembles so closely.

MUD LAKE

Mud Lake has been described in full by Welch ('36a) and by Goe, Erickson, and Woollett ('25). It is therefore only necessary here to mention the fact that the false bottom has reached the surface over part of the lake and lies within a few centimeters of the surface throughout the remainder. This lake afforded the unique opportunity of determining the vertical distribution

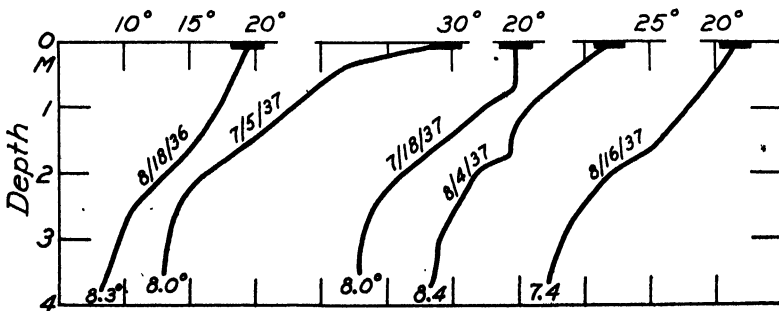


FIG. 3. Curves representing the vertical distribution of temperatures in the false bottom of Mud Lake, summers of 1936 and 1937.

of temperature in a false bottom which now virtually occupies the whole lake basin. Although the lake is about 585 meters long and about 256 meters wide and the long axis parallels the direction of the prevailing winds in that region, wave action is almost absent.

These curves are interesting in at least two respects: (1) they show a greater array of more extensive local changes in temperature on successive dates than do the curves for the other lakes studied; and (2) they show the effects of the lack of modifying influence of superimposed free water. Some of the differences shown in the curves are probably due to local temperature differences at the same level, at essentially the same position, and on the same date. Differences of this kind will be discussed later in this paper. While all of these vertical series were taken at the same station and as nearly as possible in the same position, it is not certain that the same spot was always used. Variations in the temperature readings at the bottom of the curves at essentially the same level are probably also the result of local variation.

VINCENT LAKE

Vincent Lake has already been described (Welch, '38a). It is about 480 meters long and about 360 meters broad. Since surrounding hills and forests afford considerable protection, wave action, although sometimes present, is restricted. This lake was chosen for study because of its medium size, its small amount of wave action, and its fairly deep false bottom.

While these two curves offer only an incomplete picture of the seasonal temperature situation, they do indicate something as to the form of mid-

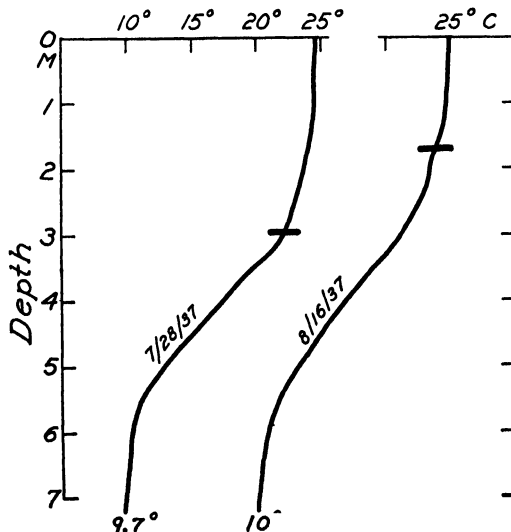


FIG. 4. Curves showing vertical distribution of temperatures in the false bottom of Vincent Lake, summer of 1937.

summer temperature distribution. A certain amount of fall in surface elevation of the lake occurred as the summer progressed (amount not measured) which accounts in part for the higher level of the false bottom on Aug. 16; also the two curves would more nearly match each other in the level of corresponding parts if the Aug. 16 curve were dropped somewhat to compensate for the falling surface level, since depth measurements were made from the surface level. In another paper, the writer (Welch, '38a) pointed out that in this lake other evidences show that at times circulation occurs to a depth of 6 meters. These curves show that this 6 meter level corresponds closely with the termination of the steep part of the temperature gradient. The upper segment of each curve indicates the almost homothermous condition of the superimposed water on these dates.

MUNRO LAKE

This lake has also been described elsewhere in some detail (Welch, '38b). It has a maximum length of about 1.6 miles and a maximum width of about 0.7 mile. These dimensions, together with a roughly ovoid shape produce a situation in which considerable wave action is common and as a result the whole lake is in complete circulation most of the time during the summer.

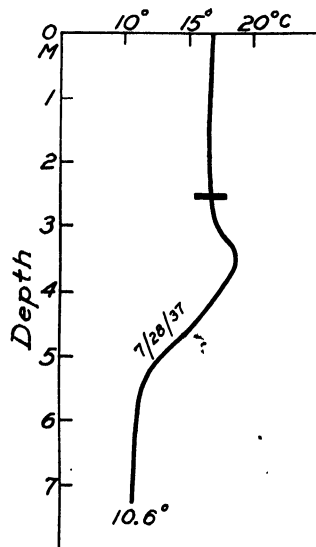


FIG. 5. Curve showing vertical distribution of temperature in the open water and in the false bottom of Munro Lake, July 28, 1937.

The form of this curve is understood when it is pointed out that a heavy all-night and all-day storm occurred on July 25 and 26 accompanied by distinctly falling air temperatures. As a result, the water above the top of the false bottom, and to a limited extent below, circulated freely, dropped in tem-

perature, and became homothermous. Convection currents presumably set up by the presence of colder, heavier water above had not yet effected a complete mixing of the warmer, lighter water below (at the level of about 3.5 meters).

DISCUSSION

Thus far, the only paper of consequence which deals with the vertical distribution of temperature in the bottom deposits of lakes is that of Birge, Juday, and March ('28). Their paper is concerned with temperatures as they occur in Lake Mendota, a large lake of considerable depth and with a bottom deposit of the common mud type. Data were secured from the deposits under water depths of 8, 12, 18, and 23.5 meters. Since the work of Birge, Juday, and March was done on bottom deposits of a very different composition and under much greater depths of superimposed water, it is interesting to compare the form of their temperature curves with those of the writer based upon bog lake false bottoms. In spite of the marked differences in the two sets of conditions, there is a striking and fundamental similarity in the form of the curves of both Birge, Juday, and March and of those of the writer for mid-summer conditions. Since the writer has been unable thus far to secure fall, winter and spring records from these same bog lakes, no further comparison can be made, but it seems probable that these bog lake curves and those of Lake Mendota have certain fundamental similarities which may hold for all of the seasons. A greater variation occurs in detail of form in the bog lake curves since the false bottom is much closer to the lake surface and thus much more subject to effects of temperature changes of the atmosphere.

Since the surface elevation of these bog lakes falls during the summer, the effect is usually that of bringing the top of the false bottom closer to the water surface. Increasing proximity to the atmosphere leads to greater range of variation in the form of the uppermost segment of the temperature curve during late summer.

In each of the bog lakes described in this paper, successive vertical temperature records were taken at the same station and as nearly as possible in the same location. However, it is obvious that it was not possible to sink the thermophone terminal in exactly the same spot previously used. Temperatures at the same levels sometimes show a variation too great to have naturally taken place in the interval since the previous records. Changes in the uppermost portion of the curves are explainable on the basis of changes in meteorological conditions, but the differences manifested in the lower portions of the curves cannot be so accounted for. In addition to these evidences of variation, vertical series of temperature records on the same date taken at different stations in the same lake (records not included in this paper) showed distinct differences in temperature at the same depth levels. Birge, Juday, and March found similar variations in bottom deposit temperatures.

of Lake Mendota and offered an explanation for the same. The writer has no evidence at this time which would justify any attempt at an explanation of the variations which occur in the bog lakes studied. It seems probable that at least one important cause may be the differences in thermal conductivity of the false bottom materials in different places at the same level since these materials are not always homogeneous in character.

SUMMARY

1. The vertical distribution of temperature in the false bottoms of five northern Michigan bog lakes in summer is presented in the form of graphs and accompanying descriptions.

2. Irrespective of the differences in the types of bog lakes studied, all of the curves have a certain fundamental similarity of form.

3. Only the upper portions of the curves reflect the variations of atmospheric temperatures.

4. In spite of marked differences in the two sets of conditions, there is a fundamental similarity in the form of vertical temperature curves for the bottom deposits of Lake Mendota, Wisconsin, to those presented in this paper.

5. The usual amount of fall in surface elevation of these bog lakes does not alter the fundamental form of the vertical temperature curve.

6. In the deeper regions of the false bottom, temperatures may differ at the same level on the same day at points at various distances apart; likewise, differences occur at similar points and levels on successive observations. It seems probable that differences in the thermal conductivity of the false bottom materials may have something to do with these temperature differences.

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ROOT HABITS OF LONGLEAF PINE AND ASSOCIATED SPECIES

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INTRODUCTION

Longleaf pine, *Pinus palustris* Miller, at one time covered an area in the south of more than 30 million acres. Today, owing to the inroads by agriculture and by other species following the cutting of the original timber, a survey in 1934 and 1935 showed that less than 80 per cent of this area is still considered longleaf pine forest land. According to this survey, about 15 million acres are in sapling- and sawlog-size stands of longleaf, nearly 2.5 million acres in reproduction, and the remaining 7 million acres are clear-cut and have failed to reproduce satisfactorily. It is estimated that nearly 30 per cent of the longleaf reproduction area is stocked satisfactorily with 900 or more seedlings per acre.¹ The remaining 70 per cent shows a low stocking of seedlings, which is principally due to destruction by uncontrolled fire, to damage by hogs, or to a lack of seed trees. The characteristic stunted condition of the longleaf pine seedlings, which lasts 4 to 10 or more years, makes them especially susceptible to fire and hogs as well as to annual defoliation by the brown-spot needle disease (*Septoria acicola* [Thüm.] Sacc.). When the pine seedlings emerge from the stunted condition, they begin rapid growth in height, and the danger of disease is considerably reduced. Since over 50 per cent of the extremely large clear-cut area (7 million acres), that must be reforested before becoming again productive, averages 3 or more seed trees per acre, while the remaining half has only 1 or 2 seed trees per acre, if the factors of destruction can be controlled, satisfactory natural reproduction should be possible on three-fourths of it.

A recent study (1938), in which the writer found that the removal of grass from the vicinity of 12-year-old longleaf pine seedlings stimulated their growth to a marked degree, suggests that the roots of the grasses compete with those of the pine seedlings and that by the removal of the grasses this competition may be eliminated, permitting the pines to develop more rapidly. This present study, therefore, was designed to determine the characteristics of the roots of the pine seedlings and of other species growing in the same area, and also to determine what relationship exists between the roots of the pine seedlings and those of the other species commonly associated with them.

¹ The estimates were supplied by the Survey Division of the Southern Forest Experiment Station.

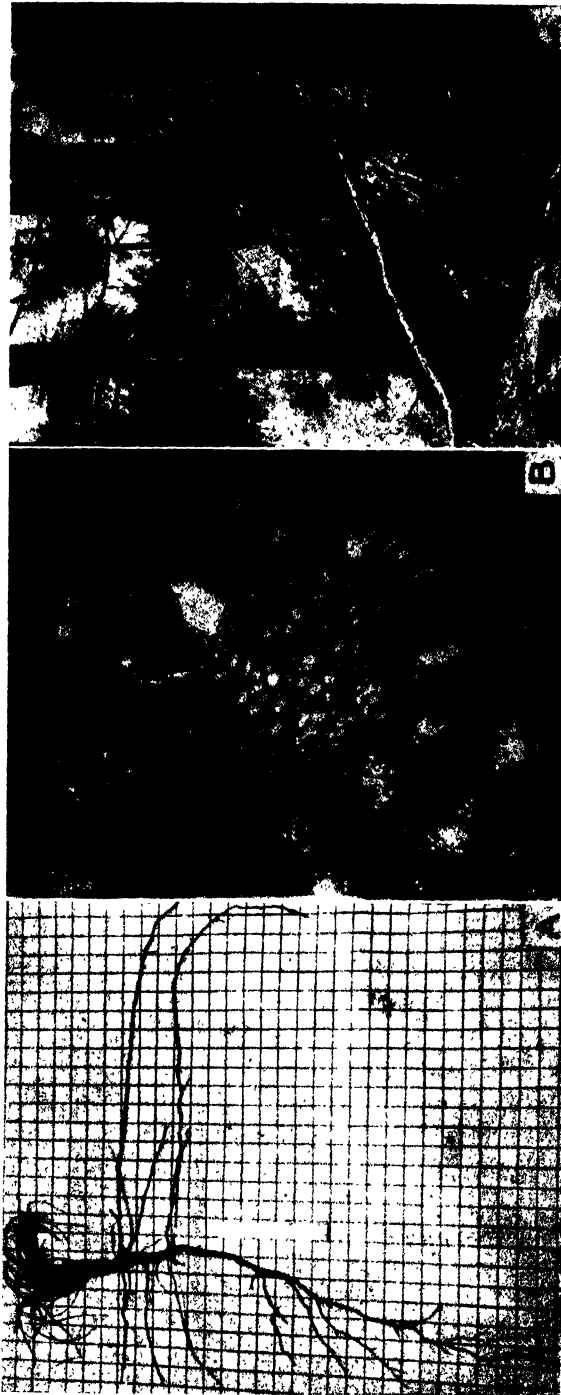


FIG. 1. Roots of longleaf pines showing:

- A. A typical root system of a longleaf pine seedling.
- B. Cross-section of an 8-year-old longleaf pine seedling cut one inch below root collar.
- C. A 12-year-old longleaf pine growing in loose soil along a railroad embankment.

GENERAL OBSERVATIONS

During the first few years following germination, a longleaf pine seedling builds up its stout root system (fig. 1A), the length and spread of which depend to a large extent on the conditions under which it grows. A cross section of the taproot just below the root collar (fig. 1B) reveals a considerable amount of organic food stored in the thick, soft cortex, in the central pith, and in the wood rays of the taproot. This often attracts hogs, which, in search of food, remove the bark from the roots and thus kill or seriously damage the pines. The roots of longleaf pine seedlings, however, are apparently able to endure unfavorable conditions. Seedlings with nearly half of their roots exposed to the intense sunlight and high temperature and showing no apparent injury other than the retardation of stem growth are sometimes found on eroded lands (fig. 2). Longleaf pine, in fact, often responds favorably to loose, loamy, well-drained soil, and makes rapid growth along railroad embankments or on fills (fig. 1C). This observation is in agreement with that reported by Weaver ('19), who found that the moisture content and the structure of the soil had considerable influence on the development of root systems.



FIG. 2. A longleaf pine seedling 11 years old with more than half of the taproot exposed to intense sunlight and high temperature, owing to the removal of the soil around it by repeated erosion.

Longleaf pine roots do not always grow symmetrically. When a root strikes a substratum unfavorable for growth, it will either turn off and grow in another direction or develop a branch that will take the lead and ultimately become the main root (fig. 3B). It is thus not uncommon to find a very short taproot with one or two terminal branches that take over the function of the taproot (fig. 3C). Sometimes a lateral branch originates near the collar, then grows parallel to the surface of the soil for some distance, and finally

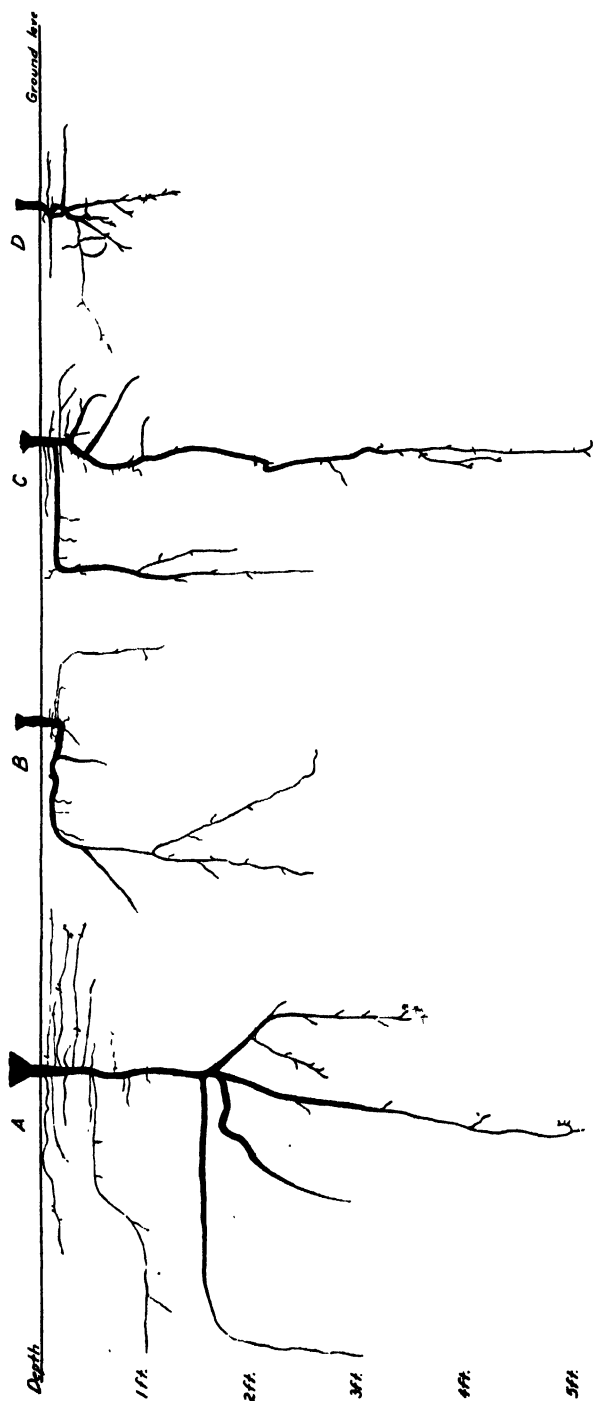


FIG. 3. Root systems of 12-year-old longleaf pine seedlings showing:

- A. Uncommon development of branches at lower depths.
- B. Lack of symmetry owing to unfavorable site conditions.
- C. Two large branches developed from the short taproot.
- D. An abnormal root system in which a branch root and the tap root have grown together, forming a loop.

grows down for a foot or more. Such a root, even though of adventitious origin, may sometimes become the main root of the tree. Although longleaf pine seedlings growing under natural conditions generally exhibit symmetry such as found in other plants with distinct taproots, because the soils of the region often contain remnants of old roots, charcoal pockets, and stiff clay, hardpans, or gravel pits, malformations of roots of pine seedlings are not uncommon (figs. 3D and 3A).

SPECIFIC OBSERVATIONS

Intensive studies were made in southeast Louisiana where longleaf pine seedlings 13 years old occurred in dense stands. Studies were also made of pine seedlings of the same age on the Harrison Experimental Forest in the DeSoto National Forest in south Mississippi. The soil type in both places was well-drained Ruston fine sandy loam. The vegetation included principally *Andropogon scoparius* Michx., *A. tener* Kunth., and *A. elliottii* Chapm., with various species of *Panicum* and legumes (table I).

The method employed in this study was essentially the same as that used by Weaver ('19), with such modifications as were necessary for the local

TABLE I. Measurements of roots of excavated longleaf pine seedlings and associated species.

Species	Number of plants excavated	Average height	Average length of taproot	Average number of lateral roots ¹	Average total length of laterals ¹	Approximate depth of most feeding roots
		Inches	Inches		Inches	Inches
<i>Andropogon elliottii</i> Chapm.....	2	—	—	8	28	10
<i>Andropogon scoparius</i> Michx.....	12	—	—	12	83.7	10
<i>Andropogon tener</i> Kunth.....	7	—	—	8.6	27.4	8
<i>Aristida virgata</i> Trin.....	2	—	—	11	37	5
<i>Cracca hispidula</i> Kuntze.....	1	—	24	6	12	4
<i>Cracca virginiana</i> L.....	1	—	14	3	24	4
<i>Crotalaria rotundifolia</i> Poir.....	1	5	10	9	7	4
<i>Galactia erecta</i> Vail.....	1	7	4	2	2	4
<i>Gymnopogon brevifolius</i> Trin.....	3	—	—	11.3	20	5
<i>Helianthus heterophyllus</i> Nutt.....	1	—	—	18	36	4
<i>Meibomia arenicola</i> Vail.....	7	6.4	9.1	5.8	11.6	6
<i>Panicum albomarginatum</i> Nash.....	1	—	—	11	18	2
<i>Panicum angustifolium</i> Ell.....	3	—	—	15	55	8
<i>Panicum ciliatum</i> Ell.....	1	—	—	16	31	6
<i>Panicum dichotomum</i> L.....	1	—	—	5	9	4
<i>Pinus palustris</i> Miller ²	19	1.5	27	26	64	4
<i>Pinus palustris</i> Miller ³	21	2.0	32	31	87	6
<i>Pinus palustris</i> Miller ⁴	34	2.0	33	14	85	6
<i>Pityopsis graminifolia</i> Nutt.....	1	—	—	12	28	2
<i>Quercus cinerea</i> Michx. ⁵	1	36	34	26	468	12
<i>Sarothra drummondii</i> Grev. & Hook...	1	—	12.5	3	12	3
<i>Smilax hispida</i> Muhl.....	1	—	—	17	300	10

¹ All root branches, whether arising from the main taproot or from lateral roots, were included under this heading.

² 13 years old, occurring in a stand with a density of 185,000 seedlings per acre.

³ 13 years old, occurring in a stand with a density of 24,000 seedlings per acre.

⁴ 13 years old, taken at random on the same site as above.

⁵ 3 years old.

conditions (Pessin, '35). It consisted of marking off a milacre quadrat, tallying the different species on it, excavating the plants with a fine, sharp-pointed tool, measuring the roots of each species, and sketching them in place. Observations were also made of the soil condition, the ground cover, and the interrelationships of the plants and their roots.

The excavations revealed, among other interesting facts, that when longleaf pine seedlings grow in dense stands, the roots tend to grow away from each other. This may be due either to the reduced soil moisture in the vicinity of the roots or to a chemotropic condition. Hooker ('15) found that roots turn toward moisture in the soil but will not penetrate a dry layer of soil in order to reach moist soil farther away. Porodko ('11) established the fact that although the curvature of roots is often due to a chemotropic response (which causes the roots to turn to, or away from, chemicals), the roots must be in contact with the chemicals before any reaction can occur. It is thus possible that either (a) the increase in the CO_2 content of the soil in the vicinity of the seedlings may produce a chemotropic effect on the roots, causing many of them to grow away from the region where the CO_2 (or H_2CO_3) is more concentrated, or (b) the decreased soil moisture within the zone near the roots caused the more aggressive roots to grow away into the regions of the soil where moisture was more abundant.

The effect of the density of stocking on the roots of pine seedlings is evident when we compare the measurements of the roots in a stand containing 185 pine seedlings per milacre with those in one containing 24 seedlings per milacre (table I). In the latter stand the taproots were longer and lateral roots were more numerous than in the former. The seedlings in the stand with the lower density were also somewhat taller than those in the one with the higher density. The effect of the density of stocking on the height growth of the stems of longleaf pine seedlings was recently reported by the writer (Pessin, '38), who found that when the height of the seedlings in the stand with the highest density was taken as 1, the following ratios were obtained:

Density (Thousand seedlings per acre)	1	5	10	15	25	50	100
Height ratio	3.5	2.7	2.0	1.8	1.3	1.0	1.0

Inasmuch as these seedlings are still under observation, no direct evidence is available on the effect of their density of stocking on the growth of the roots of the pine, but on the basis of the observations made in excavating the roots in the two quadrats with densities of 185 and 24 seedlings, respectively, it is evident that the growth in length of the roots must be as markedly affected by the density of stocking as is the height growth of the seedlings.

The roots of grasses associated with the longleaf pine seedlings in the quadrats studied were most abundant in the upper 10 inches of soil. At this depth also were found many of the fine lateral roots of the pine seedlings, from which it appears that a keen competition exists between the roots of these plants. The ability of the roots of the pine seedlings as they grow

older to penetrate deeper into the soil than those of the grasses, however, enables the pines to overcome to a certain extent the competition offered by the grasses. This is in agreement with the work of Cannon ('11) and that of Markle ('17), who found that roots of different species are distributed in different layers of the soil, thus making it possible for several different species to grow on the same area.

Characteristics of the roots of longleaf pine seedlings and of species growing on the same area

Andropogon elliotii Chapm. occurs commonly on cut-over longleaf pine lands, but it does not cover extensive areas. The fibrous roots of this plant, although generally clustered, do not form dense mats. The tough and rather coarse primary roots are grayish brown and generally grow obliquely, while the fine and profusely branched secondary roots are light yellow and often grow horizontally.

Andropogon scoparius Michx. is very abundant on longleaf pine lands and forms an important component of the longleaf pine subclimax. The roots of this species, which vary in thickness from almost hair-like to about 0.03 inch, occur generally in dense mats. The primary roots often grow straight down, while the secondary branches spread out in all directions; frequently, however, the roots grow obliquely and form a fan-shaped mass. The roots are generally light gray in color but at times are almost white.

Andropogon tener Kunth. is widely distributed but occurs mainly in large areas, where it often forms dense mats on the surface of the ground. Islands of *A. scoparius* may sometimes occur in the midst of these masses of *A. tener*, but under such conditions the former species ultimately crowds out the latter, the roots of which are rather short, dark brown, and somewhat brittle. The fine rootlets are generally of the same color.

Aristida virgata Trin., although often conspicuous, is not widely distributed. Its roots are much finer than those of *A. scoparius* and somewhat darker in color.

Gymnopogon brevifolius Trin. occurs in scattered spots, but does not form a conspicuous component of the vegetation. Its roots, which are fine, fibrous, light in color, and profusely branched, generally grow obliquely downward.

The genus *Panicum* is well represented on longleaf pine lands. *Panicum albomarginatum* Nash. occurs abundantly on moist, well-drained soils, where it forms short, bushy tufts. Its roots, which rarely penetrate beyond a depth of 2 inches, are very fine, of a light buff color, and profusely branched. The roots of *Panicum angustifolium* Ell. are much longer and somewhat coarser than those of *P. albomarginatum*, but they are of nearly the same color. *Panicum ciliatum* Ell., like most of the species of this genus, occurs in patches. Its roots, which are profusely branched and form dense mats, go down much deeper into the soil, and are considerably coarser, than those of *P. albomarginatum*. Both the primary roots and branchlets are dark brown in color.

The roots of *Panicum dichotomum* L. are very fine, light yellow in color, and occur within a few inches of the surface.

Although legumes are fairly common on longleaf pine lands, they are scattered in patches and do not cover such extensive areas as do the grasses. In open places, whether on burned or unburned areas, legumes are quite common, while in places that have been protected from fire for a long time and in which grasses have formed a dense stand, they are generally few or entirely absent.

Cracca hispidula Kuntze is not uncommon on longleaf pine lands but it generally occurs in patches. The rather long, reddish brown taproot varies in diameter from 0.08 to 0.30 inch, while the very fine and brittle lateral roots are lighter in color.

Cracca virginiana L. is common on longleaf pine lands, but is confined principally to sandy ridges. Its primary roots are long, shoestring-like, tough, elastic, and yellow in color, while the secondary branchlets are short and curly, but of the same color as the taproot.

Crotalaria rotundifolia Poir. also occurs scattered over longleaf pine lands. The light brown taproot of this species, which is about 0.1 inch in diameter, tapers towards the stem as well as towards the base of the root, where it narrows off abruptly into a fine, hair-like structure. The lateral roots are much lighter in color and branch profusely.

* *Galactia erecta* Vail. also occurs in patches but is seldom conspicuous. Its root is similar to that of *Crotalaria rotundifolia* but darker in color; the lateral roots are of the same color.

Meibomia arenicola Vail. is a very common legume on longleaf pine lands but does not cover extensive areas. Its root, like that of *C. rotundifolia*, tapers towards the stem and towards the base, where it narrows out into a fine, slender thread. For several inches in the middle it is about 0.3 inch thick. The branches begin as fine, thin roots but sometimes thicken towards the end to form swellings twice as thick as the branches. Hair-like branches grow from both the taproot and the primary branches, all of which are light brown in color.

Pityopsis graminifolia Nutt. is so abundant on lands subject to annual burning that it may serve as a good indicator of areas frequently burned over; on lands protected from fire, it is often crowded out by *Andropogon scoparius*. The roots of this species, which were found to be confined mainly to the upper 2 or 3 inches of soil, are coarse, white, and fibrous and form dense mats.

A *Pinus palustris* seedling expends most of its energy during its first few years in developing a stout, spindle-shaped taproot many times the length of the stem. As the seedling grows older (i.e., while it is still in the grass), its taproot continues to increase in both length and diameter, but its stem shows hardly any increase in size. At the root collar the root is nearly as thick as the stem above, although there is a definite annular constriction dividing the stem from the root. Below this ring, the thick, fleshy root tapers towards

the end, the thickness varying with the site condition and the age of the seedling. The long, shoestring-like lateral roots, which begin within one or two inches of the surface of the ground, may either be confined to the top foot of soil or may be found down to a depth of 3 feet or more, depending upon the site; the former condition, however, is perhaps the more common. Fine rootlets such as are frequently found on hardwood trees are not conspicuously abundant on pine roots, but the lateral roots of pines generally possess many mycorrhizae. Root-hairs are generally absent on roots of naturally grown seedlings, although under laboratory conditions they can be developed in abundance.

Quercus cinerea Michx., which occurs abundantly on cut-over longleaf pineland, often covers large areas from which longleaf pine is almost totally excluded. The roots of this plant even in the seedling stage occupy a large area. Although the stem of an excavated seedling with its branches reached only 3 feet high, its taproot was nearly 3 feet long, and the lateral roots, which were covered with fine rootlets, extended as far as 7 feet from the taproot. It is at once evident that the area from which the oak absorbs the moisture and nutrients is many times greater than that from which the pine seedling derives its nutrients and water; and this enormous root system of the small oak seedling indicates that the competition between the roots of oaks and those of pines must be very keen indeed.

DISCUSSION

When longleaf pine seedlings are in the "grass stage," that is, when their terminal growing point is on the same level or below the level of the surrounding grasses, their "feeding" roots occur at nearly the same depth as those of the grasses. Inasmuch as the number of individual grasses on typical longleaf pine lands is much greater than the number of pine seedlings, it is obvious that the absorbing surface of the grass roots is much greater than that of the pine seedlings. During periods of normal rainfall, both the pine seedlings and the plants associated with them obtain sufficient moisture, but during periods of drought, the grasses, owing to their larger transpiring surface, consume considerable quantities of soil moisture which might otherwise be taken up by the pine seedlings. This reduction of the moisture content of the soil may affect the vigor of the longleaf pine seedlings and result in the retardation of their growth. Tolskii ('13) found that moisture was the growth-controlling factor and that the depth of the lateral roots was in direct relation to the moisture content of the soil, while Pessin ('38) observed that during periods of drought the moisture content of the soil in plots with high densities was considerably lower than in plots with low densities. These differences in the soil moisture content produced differences in the growth of the roots, which in turn affected the height of the pine seedlings.

In excavating longleaf pine seedlings, it was observed that those which had started growth in height and had a typical conical terminal bud possessed horizontal roots at lower depths than the seedlings which did not possess such buds. This confirms the observations made by Laitakari ('27) that the average depth of the horizontal roots of pine is increased with the age of the trees. Heyward ('33) found in western Florida that the roots of longleaf pines were most abundant in the upper 10 inches of the soil, but he excavated roots in deep sand, while the observations reported here were made on plants growing in fine sandy loam.

Another interesting fact observed during the excavation was that under natural conditions the roots of longleaf pine seedlings made rapid growth during the spring and autumn, while during midwinter and midsummer they showed little or no indications of growth activity; this agrees with the observations made by Stevens ('31) and by Turner ('36). Of interest also is the fact that although all the excavated pine seedlings possessed mycorrhizae, they were not nearly so abundant on the roots of the naturally grown seedlings as on the roots of nursery stock, thus confirming previous observations (Pessin, '28).

In general, it may be stated that the distribution of most of the roots of longleaf pine seedlings at the same level as those of the species commonly associated with them, indicates that between the pines and the associated species exists a competition which under unfavorable climatic conditions may become so critical as to affect the growth and the vigor of the pine seedlings. Under such conditions this competition may even cause the death of many of the pine seedlings, and is thus a contributing factor to the understocking of longleaf pine stands in the South.

SUMMARY

Excavations and observations were made of more than 120 plants, including longleaf pine seedlings and grasses and herbs commonly associated with longleaf pine, on Ruston fine sandy loam in south Louisiana and south Mississippi.

It was found that under natural conditions root systems of longleaf pine seedlings display differences in symmetry. Although most root systems grow symmetrically, asymmetrical growth is not uncommon, owing to the presence in the soil of old root-holes and charcoal pockets as well as to differences in the texture of the soil.

The occurrence of most of the lateral roots of longleaf pine seedlings within the upper foot of soil, where most of the roots of the grasses and herbs associated with the pines also occur, indicates that the distribution of roots at the same depth may produce a critical competition for soil moisture during unfavorable climatic conditions. That such a competition exists is evident from the marked growth made by longleaf pine seedlings when the grasses and herbs are removed from around them.

The competition offered by the large root systems of 3-year-old *Quercus cinerea* seedlings explains the total absence or the slow growth of longleaf pine seedlings in the vicinity of oak clumps.

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STUDIES ON AMPHIBIAN ACTIVITY. I. PRELIMINARY REPORT ON THE RHYTHMIC ACTIVITY OF *BUFO AMERICANUS AMERICANUS* HOLBROOK AND *BUFO FOWLERI* HINCKLEY¹

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INTRODUCTION

The several types of activity exhibited by various animals have recently received much attention by a number of investigators, and have been relegated to the following categories by Park ('37). The beetles, *Bolcotherus cornutus* and *Megalodacne heros*, the field cricket *Gryllus* and the burrowing cricket *Stenopelmatus*, the millipede *Spirobolus marginatus*, the rodents, *Peromyscus* and *Microtus*, and certain Saturniid moths have an inherent type of activity which appears to be more or less deeply seated, and therefore not easily modified by changes in the environmental complex (Davis, '33; Johnson, '26; Lutz, '32; Park, '35; Park and Keller, '32; Park and Sejba, '35; Rau and Rau, '29).

The beetle *Passalus cornutus* has an arrhythmic type of activity under normal conditions, *i.e.* activity evenly distributed over the twenty-four hour cycle (Park, '35, '37).

The forest cockroach *Parcoblatta pennsylvanica* exhibits a type of activity in which the pattern is obviously controlled by the operating environmental influences (Park and Keller, '32).

The firefly *Photinus pyralis* and the tropical wren *Troglodytes musculus* seem to have a composite type of activity in which the influence of the environment may predominate and over-shadow an inherent rhythm (Buck, '37; Lutz, '31). Therefore any one type of activity is not confined to a particular group of animals.

As more evidence is accumulated, it becomes more apparent that the type of activity may vary with the genus and possibly with closely-related species, that one or more types of activity may be present in the same animal, *viz.* the composite pattern, and that the inherent pattern may vary in the degree of stability, *e.g.* the millipede *Spirobolus marginatus* with a deeply-seated activity pattern (Park, '35), and the rodent *Peromyscus* with a less firmly

¹The writer wishes to acknowledge his indebtedness to Professor Orlando Park under whose direction this research was done, and to Karl P. Schmidt, Curator of Reptiles and Amphibians, Field Museum of Natural History for identification of the toads.

established rhythm (Johnson, '26). In general, the arthropods seem to have more deeply-seated activity patterns than the vertebrates. Such a conclusion is very plausible since instinct may have played a more important rôle in the life and evolution of the former than the latter.



FIG. 1. A photograph showing the interior of the experimental cabinet and apparatus used in recording toad activity.

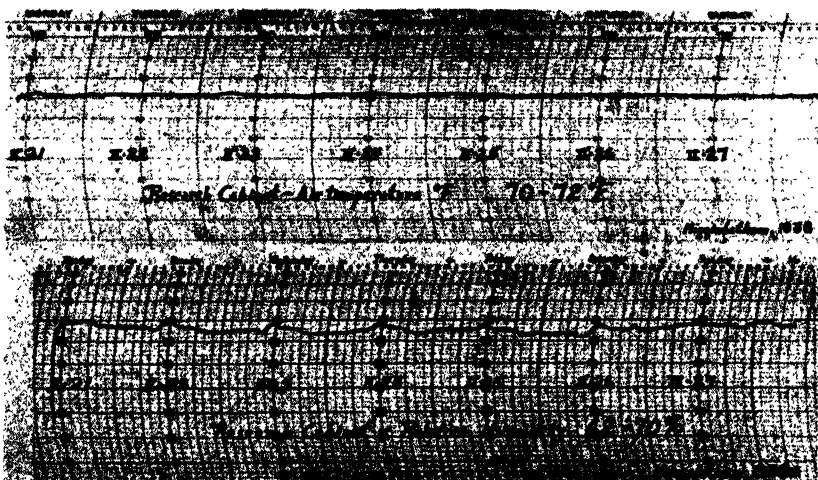


FIG. 2. Record of relative humidity and temperature in the sealed cabinet over a period of one week.

In a further examination of the problem of nocturnalism, the author began a series of experiments designed to investigate the activity of poikilothermal, terrestrial vertebrates.

The toads have long been known to be more active by night than by day. Numerous references in the literature refer to their concealment

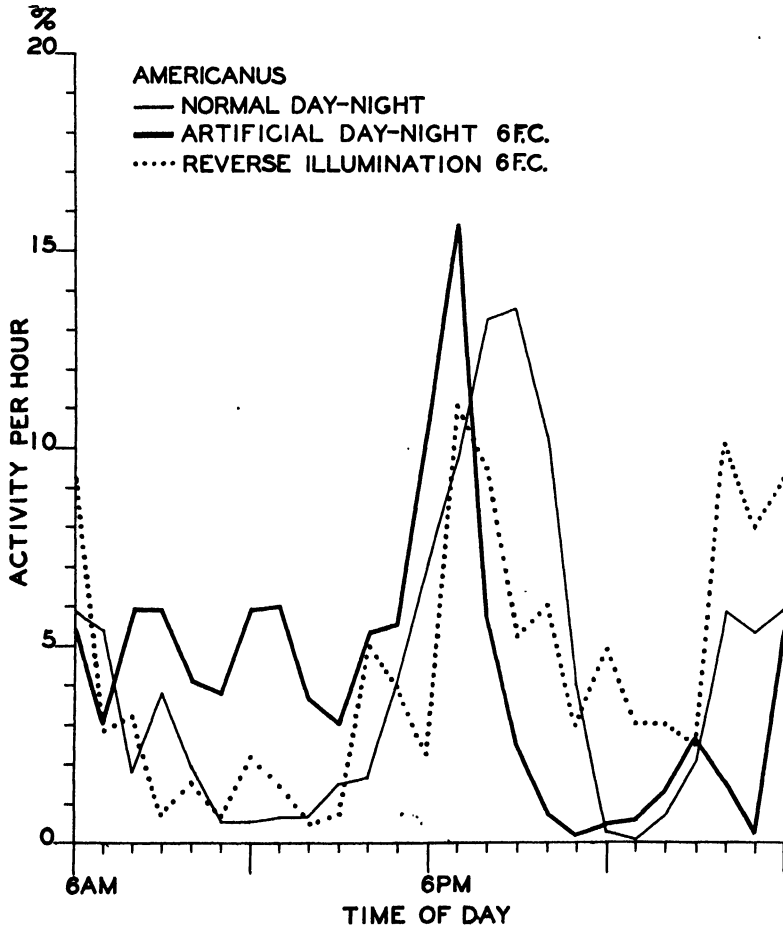


FIG. 3. Series of consecutive twenty-four hour activity records of *B. americanus* under normal day-night fluctuations of daylight, artificial day-night conditions and reversed illumination.

during the day and their appearance during the evening (Crawford, '32, '33; Dickerson, '08; Nichols, '37; Trowbridge, '37; Wright and Wright, '33). Considerable data also exist as a consequence of published collecting records of museum specimens. The evidence indicates that toads are nocturnal, but their nocturnality has not been subjected to a thorough experimental analysis. The present report is an attempt towards such an analysis.

DESCRIPTION OF APPARATUS

In an attempt to analyse toad activity in the laboratory, an experimental cabinet was constructed by remodeling a constant-temperature oven. The walls of this box consisted of a double layer of plaster-board which was supported on a wooden frame reinforced by metal. The accompanying photograph (fig. 1), showing the interior of the cabinet, renders a lengthy

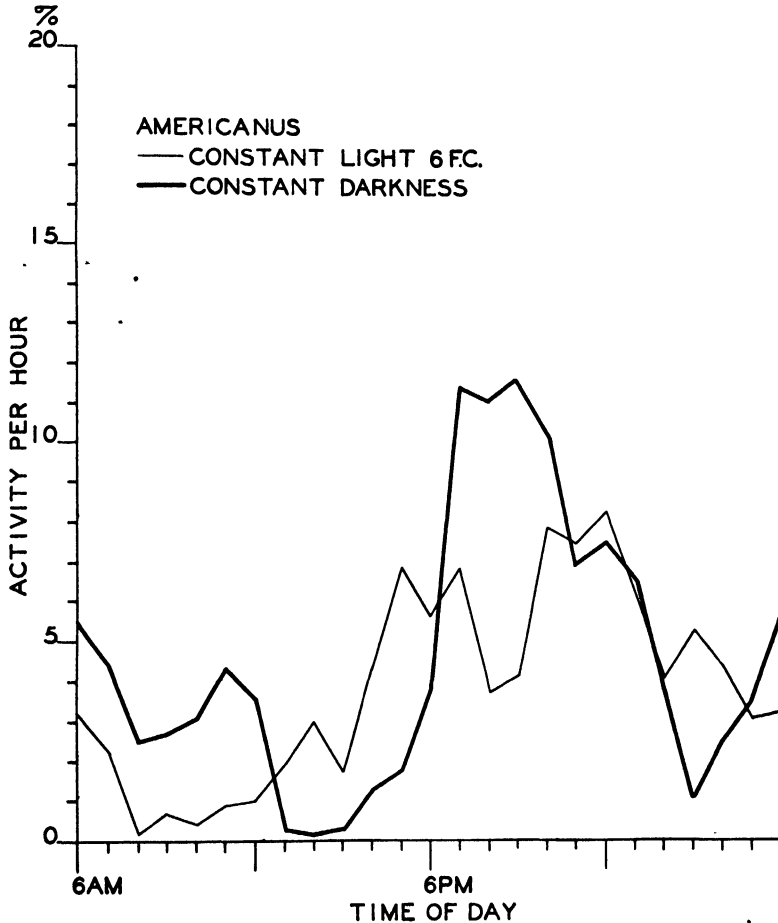


FIG. 4. Series of consecutive twenty-four hour records of *B. americanus* under constant light and in constant darkness.

description unnecessary. The apparatus for recording toad activity consisted essentially of two spring-suspended boxes in which the animals were placed, and levers for transmitting their movements to a waxed paper record carried on a kymograph drum driven by a twenty-four hour clockwork.

The cabinet was thermostatically controlled, insuring a relatively constant

temperature which did not vary over a range of 4°C . for any one series of experiments. The humidity was maintained at a relatively constant level in the cabinet by means of a battery of sponges partially submerged in water. A record of temperature and relative humidity in the sealed cabinet is shown in the following figure (fig. 2).

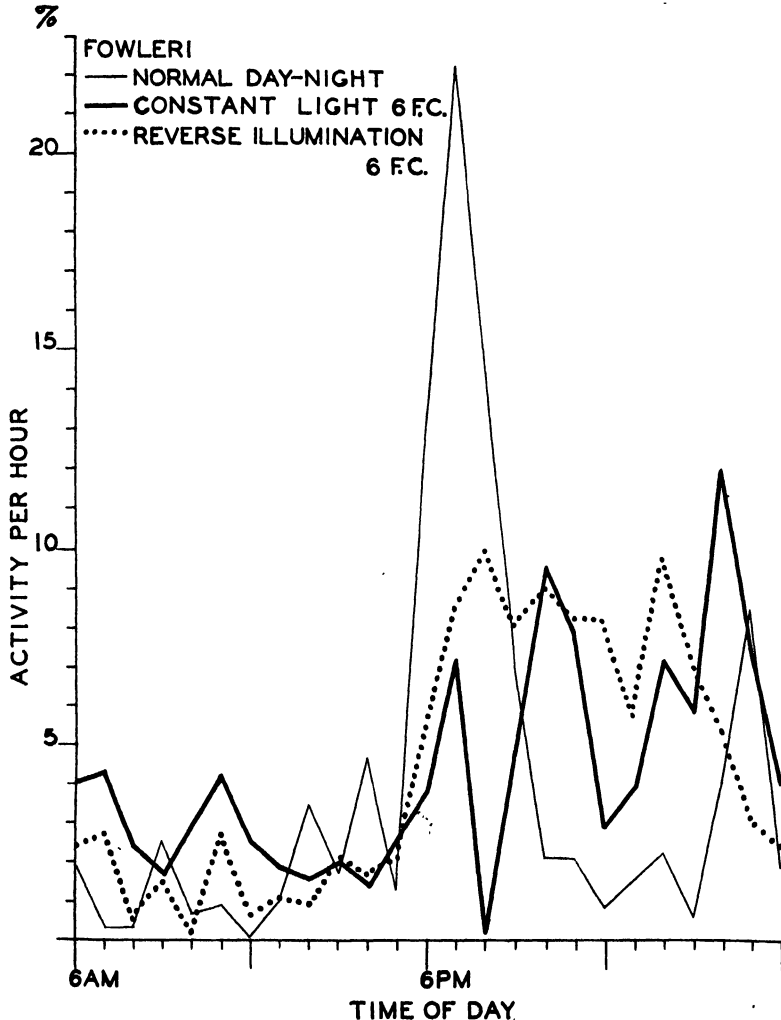


FIG. 5. Series of consecutive twenty-four hour activity records of *B. fowleri* under normal day-night fluctuations of daylight, constant light and reversed illumination.

The illumination within the cabinet was supplied by a 45-Watt bulb in some experiments, and by a 200-Watt bulb in others. The bulb was located in a triangular box built into the top of the cabinet. The beams of light passed through a half-inch stream of running water before reaching the

interior of the cabinet. Thus pronounced variations in temperature, relative humidity and ultraviolet rays were eliminated. The light intensity within the activity boxes, measured with a Weston illuminometer, was six foot-candles with the 45-Watt bulb, and ninety-seven foot-candles with the 200-Watt bulb. The illumination within the cabinet was controlled by means of a switch operated by an alarm clock outside of the cabinet. This arrangement permitted an automatic control of the duration of periods of darkness and illumination.

METHODS

In the analysis of animal activity it is desirable to record movements of one animal over a period of several consecutive days. Usually a series of

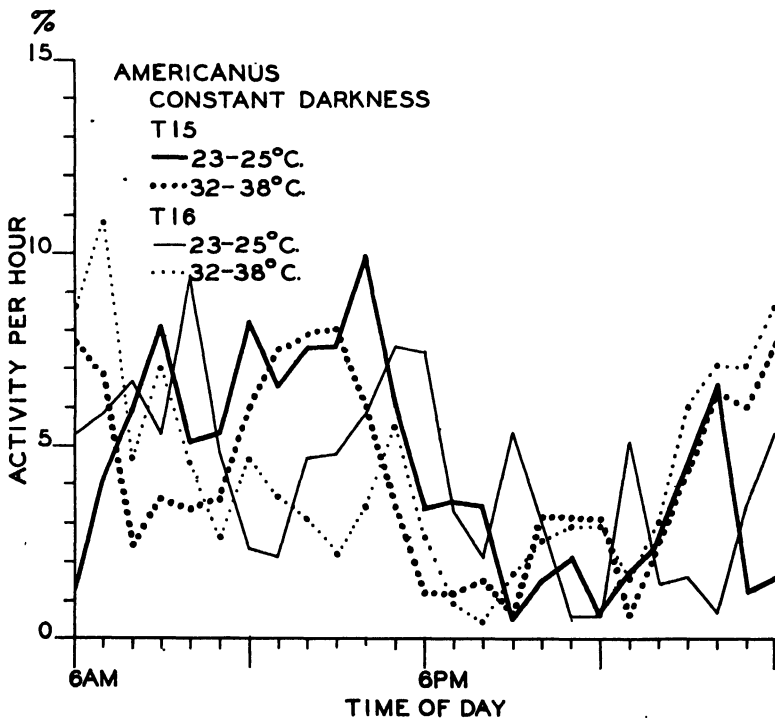


FIG. 6. Series of consecutive twenty-four hour activity records of two medium-sized individuals of *B. americanus* in constant darkness with two ranges of temperature.

ten consecutive twenty-four hour records was obtained for each experimental animal. In no case was there a series of less than six consecutive records. This procedure was necessary since some single records did not indicate the characteristic activity pattern of the animal under consideration.

In running a series of records, the experimental animals were placed singly in the activity boxes upon wet absorbent paper or damp moss. The toads were not interfered with as a rule until the end of the experiment; except for the occasional addition of a little water to the paper or moss.

Movements of the animals were recorded on a waxed paper record, and each of these deviations from the normal horizontal course of the recording stylus was considered one activity unit, and the total number of units in one hour represented the amount of activity during that time. Usually all trials run under the same experimental conditions were combined and the hourly activities converted into percentages (figs. 3, 4, 5, 6).

EXPERIMENTAL CONDITIONS

The toads used in this study were individuals of *Bufo americanus americanus* and *B. fowleri*, the two toads of the Chicago area. Nearly all of the animals were collected in the vicinity of Chicago. Some individuals, collected near Belle Rose, Louisiana, were purchased from the General Biological Supply House. In this investigation, twelve individuals of *americanus* and three individuals of *fowleri* were used, and a total of one hundred and eighty-five twenty-four hour trials was recorded (figs. 7, 8).

Activity under normal fluctuations of daylight intensity

An activity-recording apparatus similar in principle to that used in the experimental cabinet was set up in the laboratory out of range of direct sunlight. Water and a small box of sand were placed inside the activity cage with the toad.

Both species of toads were used. Nine records were taken with *americanus* and ten with *fowleri*. The results are shown graphically in figures 3 and 5, in which the per cent of activity within a given hour is plotted against the time of day. In both instances the periods of greatest activity occurred approximately between 5:00 P.M.-11:00 P.M. and 3:00 A.M.-7:00 A.M. The periods of relatively little activity occurred in the time intervals which separated the periods of greatest activity.

Activity under twelve hours of artificial light and twelve hours of darkness

Individuals of *americanus* were used in this experiment. A series of seven records was taken with one toad and eight with another. Both series were run concurrently in an illumination of six foot-candles.

The results of these records, obtained under the same conditions, indicated that one toad (T10) had a pronounced activity rhythm beginning about 4:00 P.M. and lasting until about 8:00 P.M. The other animal (T9) had a less marked activity rhythm occurring in the forenoon as indicated in figure 3. The day activity shown in this graph was due almost entirely to the diurnal activity of the toad exhibiting a morning rhythm, while the high peak of the curve is due almost exclusively to the toad showing an evening or nocturnal rhythm. Such differences in time of activity in mature toads are exceptional and appear to be due to individual differences. The same situation is some-

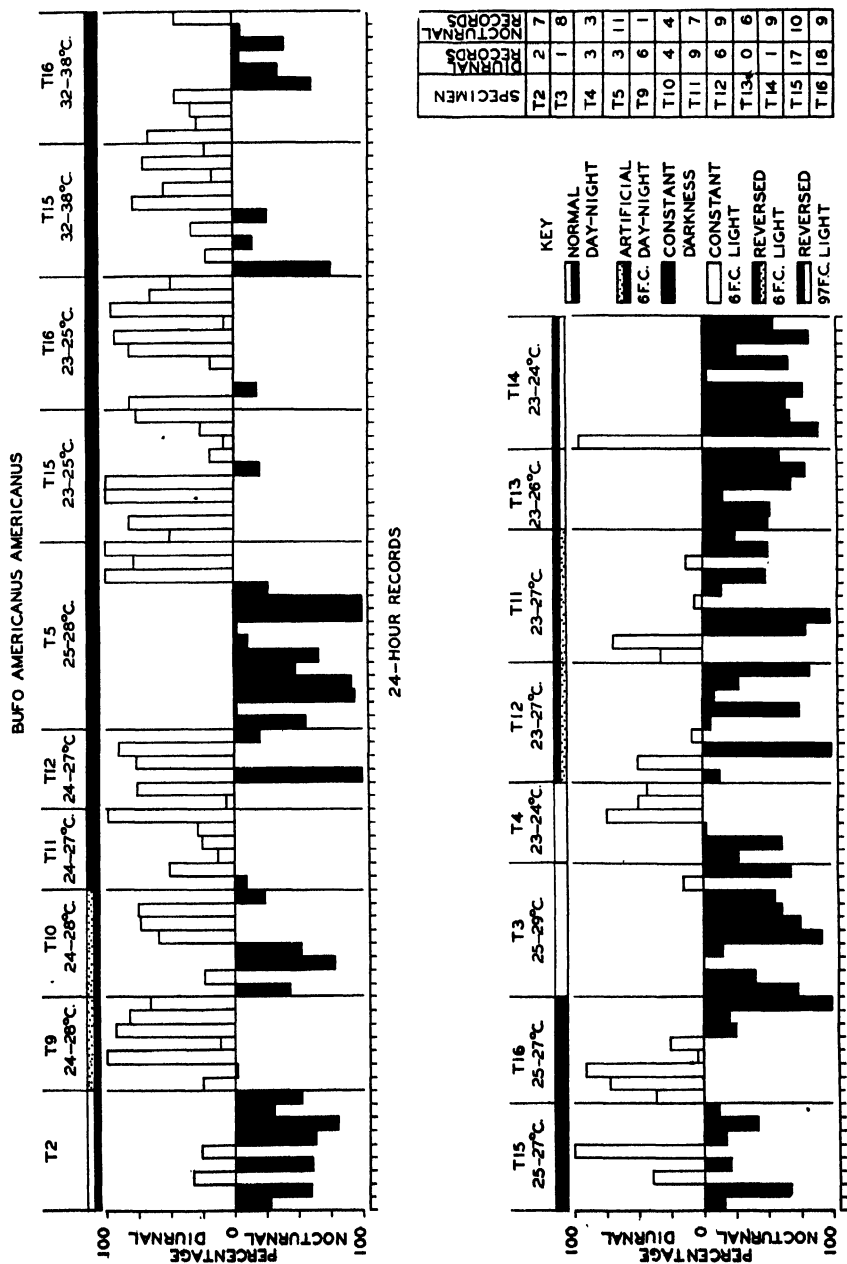


FIG. 7. Algebraic sum of activity per day of all records taken with *B. americanus*. The number of nocturnal and diurnal records of each toad is indicated in the included table.

times encountered in the field where a few toads, especially young individuals, are active during the day, but the majority emerge only at night (Crawford, '33; Noble, '31).

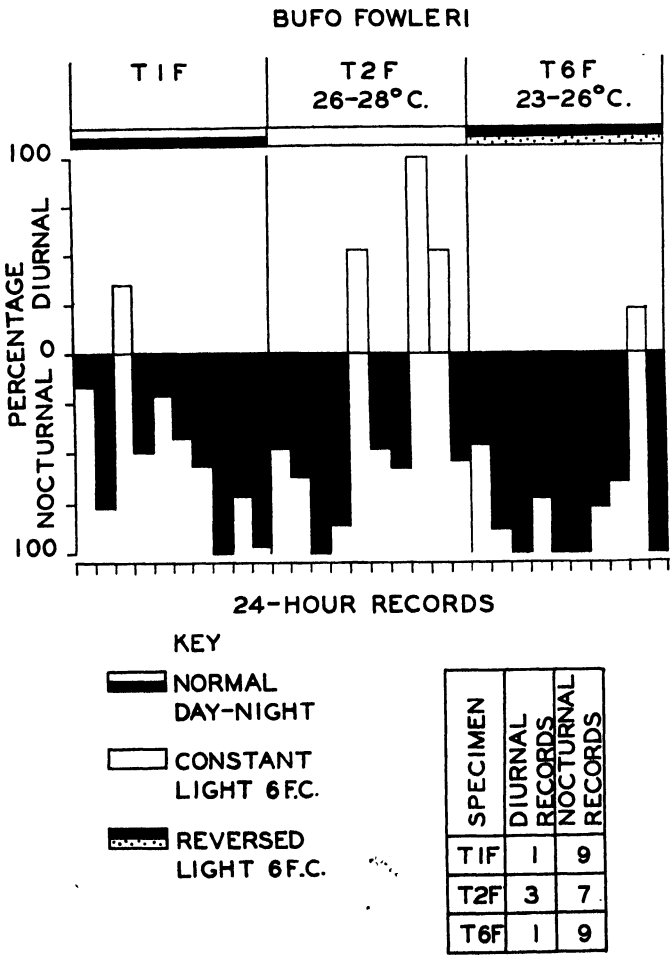


FIG. 8. Algebraic sum of activity per day of all records taken with *B. fowleri*. The number of nocturnal and diurnal records of each toad is indicated in the included table.

Activity under constant illumination

Both species were exposed to a constant light intensity of six foot-candles for several days. Sixteen records were obtained in two series (six and ten) using *americanus* (fig. 4); a series of ten records was obtained using *fowleri* (fig. 5).

In all instances the toads remained relatively quiet during the day but

became active upon the approach of dusk. The degree of activity varied throughout the night, being more pronounced in *fowleri* than *americanus*.

Activity in constant darkness

A series of fourteen records obtained with *americanus* showed a period of great activity beginning at 6:00 P.M. and lasting until 10:00 P.M.; a period of relatively less activity beginning at about 4:00 A.M. and continuing until noon; and little activity between these times (fig. 4). Eleven of these fourteen records showed a pronounced activity rhythm occurring in the evening, and three showed diurnal activity. Two other toads of this species were found to have a diurnal activity rhythm. These records are discussed under the effects of temperature on activity rhythms.

Activity under reversed illumination

Records were taken for both species under conditions of reversed illumination, *i.e.* light from 6:00 P.M. to 6:00 A.M. and darkness from 6:00 A.M. to 6:00 P.M.

Two series of records (nine and ten) were obtained using *americanus* in an illumination of an intensity of six foot-candles (fig. 3). The resulting curve follows the same general course as that for activity under normal fluctuations of daylight, *i.e.* periods of relatively high activity at dusk and dawn with little or no activity occurring during the intervening time intervals. At the end of the experiment the animals were exposed to constant darkness for six days. The records obtained under the latter conditions showed an almost complete shift from nocturnality to diurnality.

Series of records were taken with two other individuals of *americanus* (T12 and T14) under similar periods of light and darkness, and the intensity of the light was increased to ninety-seven foot-candles (fig. 7). The nocturnality of both animals was pronounced.

A series of ten trials under a light intensity of six foot-candles was obtained using *fowleri* (fig. 5). The resulting curve of activity was similar to that of *americanus* except that the activity level remained relatively higher throughout the first two-thirds of the night.

DISCUSSION

The evidence obtained in this investigation seems to indicate that the mature individuals of the common toads have an inherent nocturnal activity rhythm. However, in three individuals tested the greatest amount of activity occurred during the day. The conclusion reached experimentally that full grown toads are most active at dusk and throughout the night is supported by a great deal of field work, *e.g.* Crawford, '32, '33; Nichols, '37; Trowbridge, '37).

We found that several consecutive records gave a more accurate indication of the activity, than a group of isolated records. Occasionally a twenty-four hour record showed diurnal activity in a nocturnal individual.

With respect to light intensity, the artificial illumination used in most of these experiments was six foot-candles. This intensity in general parallels that of dawn and dusk (Park, '31). The rapid increase in light intensity at dawn and equally rapid decrease at dusk corresponds to the cessation and initiation of normal toad activity respectively. If toad activity is correlated with a low light intensity, then the various periods of illumination to which the toads were subjected experimentally should alter the time at which activity occurs. It was shown, however, that constant light, artificial day and night, and reversed illumination did not appreciably modify this pattern. Similarly a much higher light intensity of ninety-seven foot-candles, when employed under conditions of reversed illumination did not significantly alter the nocturnality of two specimens over a period of six to ten days. While the light intensities used in this preliminary study may not greatly affect the rhythmic activity of toads, much higher intensities or less understood radiations may alter the activity pattern.

The effect of hunger and fatigue on activity is of interest, and is being investigated at the present time. In almost all of the records the toads were usually most active during the first twenty-four hour period. After the first day in the experimental cabinet the toads generally were much less active. In most of the cases a much greater amount of the activity occurred at night, particularly at dusk, and this period of activity was characterized by alternating active and quiescent intervals. After the first three or four records the effects of fatigue could be observed as a decrease in the number of activity units per hour, and in the number of active periods occurring in the twenty-four hour cycle, as has been demonstrated with other animals (Park, '35). These effects were particularly evident in toads which had not eaten for a few days previous to the experiment.

For purposes of testing the effect of temperature on activity rhythms of toads, two medium-sized individuals of *americanus* (T15 and T16) were tested for a period of ten days in constant darkness at 23–25° C. and found to have diurnal rhythms. The temperature of the experimental cabinet was increased about ten degrees (32–38° C.) and records taken for ten more days. At the termination of this period the temperature of the cabinet was dropped to the range of 25–27° C. and records taken for eight additional days, and at this point one toad died and the other was too weak for further experimentation. It is notable that a doubling or even a tripling of the number of activity units occurred in one hour when the temperature was increased about ten degrees, and there was some change from diurnality to nocturnality (fig. 7), although the peaks of activity remained relatively unchanged (fig. 6). Kalmus ('34) found that the "time-memory" of bees

was not appreciably altered at ordinary temperatures. It is evident that this phase of the problem needs further experimental analysis.

A moderately high relative humidity was maintained in the experimental cabinet. Since toads are sensitive to moisture (Noble, '13), and are known to react positively to a moist atmosphere (Shelford, '13, '14), it is possible that the increase in relative humidity at dusk in nature plays an important rôle in establishing and maintaining their nocturnality. This is an aspect of the problem which is at present being investigated.

SUMMARY

Toads are commonly observed to be more active by night than by day. In an attempt to analyse toad activity in the laboratory, records were taken under normal fluctuations of daylight intensity and in an experimental cabinet in which temperature and relative humidity were held relatively constant while the periods of illumination were varied. In all of these experiments the movements of the experimental animals were transmitted to twenty-four hour kymograph drums carrying waxed recording paper. Activity records of *Bufo americanus americanus* and *Bufo fowleri* were taken usually for a period of ten consecutive days. Data obtained under normal fluctuations of daylight, constant light, constant darkness, and reversed illumination indicate an inherent activity rhythm in mature individuals.

Of twelve individuals of *americanus* tested, one mature and two young toads were found to be diurnal. This occasional diurnality in mature toads is sometimes observed in the field. Very young toads are generally regarded as diurnal.

In the case of the two young toads it was found that an increase of ten degrees Centigrade usually doubled or tripled the amount of activity in any hour but did not greatly affect the distribution of their activity.

Relative humidity is a possible influence in modifying the behavior pattern of toads. It is thought probable that this influence is important in establishing and maintaining the nocturnality of mature individuals.

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A STUDY OF THE TOLERANCE OF TREES TO BREAKAGE BY ICE ACCUMULATION

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On January 7, 1937, a sleet storm in portions of Missouri and Illinois resulted in the greatest load of ice on the trees in the history of the region. The intensity of the storm seems to have been greatest in west central Illinois from Quincy to Rushville. Press reports following the storm stated that, "Trees are ruined," and, "There was scarcely a tree escaped the ravages of the ice." This is hardly to be taken as editorial exaggeration as the noise of breaking trees during the night and the debris of branches that blocked every street in the city must have been impressive.

The writer spent three days in Rushville during late March of that year making a general survey of the damage to the various species of street and lawn trees. A total of 979 individuals of 52 different species were observed and classified as badly broken, moderately injured, or escaping with little or no injury. Time did not permit careful study of the damage, but the survey showed such marked differences in resistance of species to the ice load that it seemed worth while to report the findings. The species are arranged in the following table in the order of their susceptibility.

DISCUSSION

No study was made to discover the characteristics that determined susceptibility to ice accumulation and consequent breakage. Examination of the data indicates that growth habit of the tree is possibly an important factor. The heavy injury sustained by a number of finely branched species suggests the hypothesis that the amount of surface presented by the branches as focal points for ice accumulation is of considerable importance. However, the data on some of these species are so limited that no definite conclusion is warranted. There are many other varying factors such as the age of the trees and the exposure to the storm.

Examination of the literature reveals very few studies that might throw light on the problem. The available studies are largely on European forest species. Vorreiter ('37) found the strength and specific gravity of the wood to be the important factor in determining the extent of breakage of spruce trees by snow and ice. While this is doubtless a factor in the breaking of trees, whatever the cause, it cannot explain the losses from this sleet storm,

TABLE I. *Susceptibility of trees to breaking by ice accumulation*¹

Species	Number examined	Per cent injured little	Per cent injured moderately	Per cent badly broken
<i>Salix babylonica</i>	2	0	0	100
<i>Betula alba</i>	3	0	0	100
<i>Betula lutea</i>	5	0	0	100
<i>Ulmus americana</i>	111	6	10	84
<i>Populus deltoides</i> and hybrid poplars	34	9	41	50
<i>Betula pendula</i>	10	10	30	60
<i>Acer saccharinum</i>	117	11	21	68
<i>Platanus occidentalis</i>	6	17	33	50
<i>Castanea dentata</i>	11	27	46	27
<i>Populus nigra</i> var. <i>italica</i>	29	34.5	31	34.5
<i>Pinus strobus</i>	11	36	9	55
<i>Prunus armeniaca</i>	29	38	17	45
<i>Acer saccharum</i>	102	41	26	33
<i>Prunus</i> sp. (Cherry)	26	42	16	42
<i>Robinia pseudo-acacia</i>	11	55	9	36
<i>Juniperus virginiana</i>	88	55	19	26
<i>Liriodendron tulipifera</i>	7	57	43	0
<i>Pyrus malus</i>	37	73	16	11
<i>Carya ovata</i>	4	75	0	25
<i>Tsuga canadensis</i>	4	75	0	25
<i>Acer negundo</i>	8	75	25	0
<i>Diospyros virginiana</i>	21	76	24	0
<i>Picea abies</i>	39	77	18	5
<i>Acer platanoides</i>	9	77	23	0
<i>Thuja occidentalis</i>	29	79	14	7
<i>Quercus alba</i>	10	80	0	20
<i>Salix discolor</i>	7	86	14	0
<i>Pinus sylvestris</i>	7	86	14	0
<i>Prunus</i> sp. (Plum)	18	89	11	0
<i>Catalpa speciosa</i>	36	94	6	0
<i>Pyrus communis</i>	30	97	3	0
<i>Juglans nigra</i>	48	98	2	0
<i>Pseudotsuga taxifolia</i>	2	100	0	0
<i>Pinus nigra</i>	3	100	0	0
<i>Magnolia tripetala</i>	3	100	0	0
<i>Gleditsia triacanthos</i>	5	100	0	0
<i>Ailanthus glandulosa</i>	42	100	0	0

¹ Single individuals of the following species were examined and the amount of injury noted as follows:

Injured little—*Fagus grandiflora*, *Carpinus caroliniana*, *Prunus serotina*, *Gymnocladus dioica*, *Magnolia acuminata*, *Acer rubrum*, *Maclura pomifera*, and *Picea pungens*.

Injured moderately—*Cornus florida* and *Celtis occidentalis*.

Badly Broken—*Tilia americana*, *Ulmus fulva*, *Quercus velutina*, and *Prunus persica*.

as *Ailanthus* and *Catalpa* with light weak wood suffered little injury. Windirsch ('36) reported that trees with cylindrical crowns suffered less bole injury than those with conical crowns. Haufe ('34), who studied the effects of a heavy coating of ice that remained on the trees in the Erzgebirge for a period of four weeks and destroyed 300,000 cubic meters of timber, found that trees with long symmetrical crowns suffered less than those with short or one-sided crowns. These authors make certain recommendations for silvicultural practice, but their findings are limited to few species and throw very little light on the data reported in this study.

In view of the great importance of *Ulmus americana* L. as a street tree, the heavy damage to this species is especially noteworthy. The damage to *Acer saccharinum* L. is not surprising as experience has shown that this species also breaks badly during wind storms.

It is obvious that breaking is not necessarily fatal to trees. If the wounds are properly cared for, the effect, in some cases, is similar to that of heavy pruning. During the subsequent growing season, many of the injured trees reported in this study made a reasonable good recovery.

It is to be regretted that time did not permit a study of the injury to forests in this region which, according to reports, was heavy.

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FACTORS INFLUENCING THE OXYGEN CONSUMPTION OF SEVERAL SPECIES OF PLETHODONTID SALAMANDERS IN AËRIAL AND AQUATIC MEDIA¹

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The plethodontid or lungless salamanders breathe by means of exchange of gases through the highly vascular moist surfaces of the mouth and pharynx cavity (buccopharyngeal respiration), as well as by cutaneous respiration over the whole surface of the body which is well supplied with superficial capillaries. The evolution of the lungless salamanders coincided with the adoption of the mountain brook habitat, and it was only subsequently that they spread out into a more terrestrial type of existence (Noble, '31). The problem arose concerning whether there might be different oxygen requirements for the present land species as compared with the so-called aquatic species. Such differences if present might account for the differential distribution since both types have the same kind of mechanism for securing oxygen. A further problem was suggested from the fact that, in captivity, the salamanders frequently clump together in loosely knit groups. Salamanders have strongly thigmotactic responses and will crawl inside of glass bottles or under stones or sticks placed in their vicinity, and the tendency to group together may well be a manifestation of this thigmotactic response. However, it seemed worth while to determine whether such a grouping might have any effect on their oxygen consumption. It has been demonstrated that aggregation does affect the oxygen consumption of certain animals (Allee, '27).

With these points of departure for experimental procedure, the problems outlined above were investigated. That relating to species requirements had been begun in 1930-31 at the American Museum of Natural History under the direction of G. K. Noble. These early experiments served to show the necessity of more perfectly controlled conditions than were available up to that time. The work was continued at the University of Chicago during the years 1932-36, with carefully controlled conditions, and only the experiments

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I am also indebted to Dr. G. K. Noble of the American Museum of Natural History for initiating my interest in plethodontid salamanders and the problems relating to their habitat selection.

performed under the improved conditions are included in this report. This phase of the work was under the direction of W. C. Allee and stresses the possible aggregational effects.

The species tested include *Plethodon cinereus* (collected in northern Indiana), *Eurycea bislineata bislineata* (from central Indiana), *Desmognathus fuscus fuscus* and *Desmognathus fuscus ochrophaeus* (from northwestern Pennsylvania and northeastern Ohio), and *Gyrinophilus porphyriticus* (from western New York). The animals maintained as a stock supply were kept in covered glass moist chambers containing damp moss (or damp filter paper in a few cases). The chambers were placed in the constant temperature room in which the experiments were performed. They were fed on white worms (Enchytraeidae) or earth worms, usually about once a week, and experiments were made on animals about a week after feeding in most cases.

METHODS

The methods used for determining oxygen consumption of salamanders in an aerial and in an aquatic medium have been fully described² (Wilder, '37). Using the same equipment, with the addition of a Van Slyke gas analysis apparatus only, Miss Wilder adequately demonstrated that results obtained by the two methods as used in 1935-36 are entirely comparable. The apparatus used for testing oxygen consumption in air, consisted when first used, of a series of glass respirometers, each composed of a flask of about 140 cc. capacity connected by ground-glass connections with a water manometer mounted on a wooden frame and having one other inlet through a ground-glass stopcock. A small glass cup designed to contain 2 cc. of 30 per cent KOH was attached inside the dome of the respirometer. This provided for the absorption of CO₂. This was the form of the apparatus used from June through August 1932 and in 1933 up until July 23, when the apparatus was modified with the addition of an extra stopcock as outlet, so that a current of air could be drawn through the chamber between tests without reassembling the apparatus or disturbing the animals. Seven such respirometers were available for the work, one of which was used as a blank and the other six for the tests. All were set up in a row in a room in which the temperature was under positive control to within a degree centigrade. The barometric pressure was recorded to the nearest tenth of a millimeter and the temperature to the nearest tenth of a degree C. at the time of each manometer reading. Since the presence of the observer in the constant temperature room when readings were taken caused the temperature to fluctuate rather rapidly, the set-up was amended by immersing each of the respiration chambers in a beaker of water for the duration of the test period. This change was not made, however, until the spring of 1933. The work

² Miss Janet Wilder deserves special credit for the arduous task of correlating the two methods used, without which certain comparisons made here could not be drawn. . .

was dropped in December of 1933 until the fall of 1935, when, in place of using individual beakers of water, a large metal vat was constructed and the respirometers, supported on their ring stands, were immersed together in the vat, with the level of water covering the bell of the air chambers. The total amount of oxygen consumed was calculated from the change in manometer levels (of experimental chamber and blank) and the volumes of air involved, according to the following formula:

$$\Delta V = \left[(V_{1s}) \times 0.3592 \times \left(\frac{P_{1s}}{T_1} \right) \right] \left[\frac{\Delta P}{P_{2B}} \right].$$

Delta V = volume decrease (at S. T. P.) = total amount of oxygen consumed. V_{1s} = volume of respirometer in which salamander is tested minus volume of salamander³ and KOH. P_{1s} = Pressure inside respirometer at the start (barometric minus water vapor pressure). P_{2B} = Final pressure inside blank respirometer (barometric minus water vapor pressure minus reading of blank manometer reduced to millimeters of mercury). T_1 = Temperature of water bath (°C.). *Delta P* = Manometer reading of test respirometer minus manometer reading of blank at end of test (reduced to millimeters of mercury). $0.3592 = \frac{273}{760}$ (Standard temperature and pressure factors). Results are reported as cubic millimeters of oxygen consumed per gram of animal per hour.

The following method was used for oxygen consumption determinations in the aquatic medium. Erlenmeyer flasks of known capacity, each equipped with a siphon and rubber stopper, were used for the respiration chambers. At the close of the experimental period, during which the flasks were kept in the constant temperature water bath, a sample of water was taken from each test flask and from a blank, and analysed by the permanganate modification of the Winkler method for determining dissolved oxygen in water (Standard methods, '33). On the basis of the analyses the total amount of oxygen (at S. T. P.) consumed by the animals was calculated, and results reduced to cubic millimeters of oxygen per gram per hour.⁴

TESTS IN AIR

The array of factors influencing the oxygen consumption of an individual or of a species is considerable, and the importance of all of them was not completely realized during all stages of the experimentation. It is a well

³ In calculating the volume of the salamander its specific gravity was considered as 1.0. Its weight in grams was therefore used as its volume in cubic centimeters.

⁴ Yonge ('37) has recently called attention to an error introduced into oxygen consumption experiments by the absorption of oxygen by mucus. This point might be of importance in work on salamanders as they secrete much mucus under certain conditions. It is not probable, however, that the results obtained were much affected by this phenomenon, as the secretion of mucus is not pronounced except by exposure to chemical irritants.

known fact that temperature is very important in influencing the metabolism of cold blooded animals (Vernon, '97) and the effect of temperature was easily demonstrated. In tests on *Eurycea bislineata bislineata* and *Desmognathus fuscus fuscus* using the respirometer method, a decrease of 10° C. was accompanied by a decrease in oxygen consumption to about one-third of what it was at 19° C. Within the limits tested these results are roughly in accordance with Van't Hoff's principle.

In order to evaluate the importance of several of the other factors which might influence oxygen consumption, a large series of tests was made on *Plethodon cinereus* in 1932-1933, using the respirometer in its earliest form. In all these tests the sexes were kept separate. In order to ascertain the sex of the small plethodontid salamanders it is necessary to anesthetize them and examine the cloacal region for the appearance of cloacal glands. This process was omitted and sex was ignored as a factor after the large series of tests showed no appreciable difference between the results for males and females.

By far the largest number of tests on *Plethodon cinereus* in 1932-33 were made in an attempt to find out the effect of numbers present on individual oxygen consumption. It has been demonstrated (Allee, '31) that in certain forms this is an important factor in regulating the activity of the individuals and their resultant oxygen consumption. Table I (Sections A, B and C) shows the results of the experiments made in the summer of 1932 within two months after the time the animals were collected. A total of 186 tests on 29 groups of 3 or 4, and 192 tests on 30 isolated individuals, gave no significant difference between results for groups and singles ($P = 0.1054$)⁵ although the experiments at 15.5-16.0° indicated higher oxygen consumption for the groups. The averages for the entire 1932 series were 45.6 ± 0.6 cu. mm. oxygen per gram-hour for groups and 43.5 ± 1.1 cu. mm. oxygen per gram-hour for singles. In this series of experiments the test period for the groups and isolated individuals was the same, averaging 12.6 hours duration. During this time there was a greater change in water levels in manometers of the respirometers of the groups than in manometers of the singles. Since the maximum efficiency of the respirometers could be obtained by allowing the tests to run long enough to get the greatest change in water levels in the manometers, the experiments in the summer of 1933 were conducted to allow as great a change in height of the water column of the respirometers in which isolated individuals were tested, as in those of the groups.

⁵ P = Statistical probability as determined by "Student's" method for determining statistical significance of relatively small numbers of paired comparisons. A value of 0.05 represents five chances in one hundred of getting as great a deviation by random sampling as the one observed. This corresponds to three times the probable error of the mean difference and is considered the upper limit of statistical significance; the smaller this fraction, the greater the significance.

TABLE I. Oxygen consumption of five species in air at all temperatures tested; comparison between grouped and isolated individuals.

Species	Temp. °C.	GROUPS						SINGLES					Statis. probab.	No. of paired comparisons ^a
		Average time in each test (hrs.)	No. of tests	No. of groups	No. in group	Average wt. (gms.)	Oxygen consumed (cu. mm. per gm.-hr.)	Average time in each test (hrs.)	No. of tests	No. of indiv.	Average wt. (gms.)	Oxygen consumed (cu. mm. per gm.-hr.)		
A. <i>P. cinereus</i> (1932).....	15.5-16	13.6	102	15	3-4	0.97	43.4±0.6	13.6	102	15	0.99	39.4±1.2	0.0400	5
B. <i>P. cinereus</i> (1932).....	20 -20.5	11.6	84	14	4	0.94	47.8±0.3	11.6	90	15	1.00	47.6±1.1	0.9252	5
C. <i>P. cinereus</i> (av. for 1932).....	15.5-20.5	12.6	186	29	3-4	0.96	45.6±0.6	12.6	192	30	1.00	43.5±1.1	0.1054	10
D. <i>P. cinereus</i> (1933).....	18.5-19.5	17.0	80	11	3-5	0.91	44.8±0.9	38.8	78	21	0.94	44.1±2.2	0.7762	6
E. <i>D. f. ochrophaeus</i>	14.5-19.5	12.7	54	11	3-4	1.20	43.2±1.7	26.4	110	33	1.31	45.0±1.7	0.4468	9
F. <i>D. f. fuscus</i>	16.2-16.8	7.7	23	8	3-4	2.48	39.5±2.3	20.6	100	30	2.53	38.4±1.3	0.6324	8
G. <i>E. b. bislineata</i>	15.0-16.7	10.4	21	7	3-4	1.05	52.4±1.9	26.8	61	24	1.17	57.6±1.3	0.1220	7
H. <i>G. porphyriticus</i>	14 -16.7	6.2	17	7	2	12.0	18.0±1.0	11.1	17	7	12.4	15.2±0.5	0.1302	5

^a In making these comparisons the average results for all of the groups tested in one "series" constituted one of the pair and the average results for the singles tested at the same time constituted the other. A "series" sometimes lasted for several days with a number of tests made on the same animals without re-assembling the apparatus. For all of the experiments following those with *P. cinereus* fresh air was blown through the respirometers between tests as explained in the section on methods.

^b ± represents the probable error determined by the usual methods. The values used in computing the standard deviation and probable error were not the results of each test, but the averages for the results of tests on groups or singles in each "series." The number of values used in each case was equal to the number of paired comparisons.

This was accomplished by conducting the tests simultaneously with those of the groups as before, but having fewer tests of longer duration for the singles, compared with more tests of shorter duration for the groups. The results are given in Table I (D). The averages in this case were 44.8 ± 0.9 cu. mm. per gram-hour for 80 tests on 11 groups of from 3-5 and 44.1 ± 2.2 cu. mm. per gram-hour for 78 tests on 21 individuals tested singly. The difference is not significant ($P. = 0.7762$).

Similar tests were repeated for four different species using the respirometer method in the final form. The results are given in Table I (E-H) which includes comparisons between grouped and isolated individuals at all temperatures at which such tests were made. There is considerable variability in the values obtained for oxygen consumption, but there is no definite trend of differences between the grouped and isolated individuals, and within each species the results are not statistically significant.

TESTS IN WATER

In the first tests that were made on *Desmognathus fuscus fuscus* in an aquatic medium, there was apparently a significant difference between the oxygen consumption of groups of 3 or 4 as compared with isolated individuals (Table II, A). Eleven experiments were conducted at 17° C. over a test period of two hours. The individuals to be grouped and isolated were chosen at random. The groups consumed on the average 48.3 ± 1.1 cu. mm. oxygen per gram-hour and the singles 53.1 ± 1.3 cu. mm. per gram-hour. The difference has a statistical significance of 0.0264. There is one important factor, namely oxygen tension, which does not remain constant for the groups and singles in this experiment. Since all of the tests were run for the same length of time and in the same sized containers, the oxygen tension was reduced further, during the course of a test, in the case of the groups than for the singles. The experiment was repeated at a later date, using a larger flask and a slightly shorter time (calculated to provide the same oxygen tension for both the groups and singles at the end of the test period) with the result that the apparently lower oxygen consumption of the groups in the preceding tests, was now replaced with an apparently lower oxygen consumption of the singles (Table II, B), although in the later experiments the difference was not statistically significant ($P. = 0.0734$).

Similar results were obtained with a different subspecies, *Desmognathus fuscus ochrophaeus*, using equal times and amounts of water for the groups and singles (Table II, C). The average values obtained are 49.8 ± 1.2 cu. mm. oxygen used per gram-hour for 10 groups of 4, and 54.1 ± 1.7 cu. mm. oxygen per gram-hour for 40 isolated individuals. The difference is statistically significant ($P. = 0.0224$). This series was not repeated but from the nature of other evidence which indicates that salamanders are very dependent on the oxygen tension of the aquatic medium, it seems safe to

TABLE II. Comparison between oxygen consumption of grouped and isolated individuals of four species tested in an aquatic medium.

Species	Temp. °C.	GROUPS						SINGLES						No. of paired comparisons ⁸		
		Time (hrs)	No. of tests	No. in group	Av. wt. (gms.)	O ₂ tension (cc. O ₂ per l.)		Oxygen consumed (cu. mm. per gm.-hr.)	Time (hrs.)	No. of tests	Av. wt. (gms.)	O ₂ tension (cc. O ₂ per l.)			Oxygen consumed (cu. mm. per gm.-hr.)	Stats. probab.
						at start	av. at end					at start	av. at end			
A. ⁹ <i>D. f. fuscus</i>	17	2	11	3-4	2.37	5.9	3.2	48.3±1.1	2	44	2.62	5.9	5.0	53.1±1.3	0.0264	11
B. ¹⁰ <i>D. f. fuscus</i>	16.5-17.6	1.74	11	3-4	2.50	6.0	5.2	54.5±1.3	2	42	2.53	6.0	5.3	50.8±1.9	0.0734	11
C. ⁹ <i>D. f. ochrophaeus</i> .	17	2	10	4	1.56	5.7	4.1	49.8±1.2	2	40	1.50	5.7	5.3	54.1±1.7	0.0224	10
D. <i>G. porphyriticus</i> (ad.).....	16.5-17.0	0.78	12	3-4	12.4	6.4	5.4	29.0±1.0	1.1	44	12.4	6.4	5.3	28.1±1.0	0.3434	10
E. <i>G. porphyriticus</i> (la.).....	14.6-17.5	1.02	6	4	4.7	6.1	5.2	41.8±1.2	1.5	20	4.7	6.1	5.3	34.4±1.4	0.0362	5
F. <i>G. porphyriticus</i> (la.).....	16.5-17.0	1.67	5	5	2.5	6.3	5.4	48.2±0.8	2	25	2.5	6.3	5.7	48.8±2.6	0.8512	5
G. <i>E. basileala</i>	16.0-17.5	1.49	14	4	1.21	6.5	5.6	110.9±2.2	2	56	1.21	6.5	5.9	91.4±2.0	0.0000	9

⁸ For each comparison the results of a test on one group were compared with the average results of tests on the same number of animals tested singly. When more than one test was made on a group or on the singles the results were averaged. Otherwise the number of tests for the groups is the same as the number of paired comparisons.

⁹ Tested in the same size vessels and for the same length of time.

¹⁰ Tested at same oxygen tension.

conclude that the difference in oxygen consumption first attributed to the effect of the group itself, must be due to the lowered oxygen tension in the flasks containing the groups.

A series of experiments carried out with a still different species, *Gyrinophilus porphyriticus*, serves to illustrate the dependence of these salamanders on oxygen tension. In table III, the results are given for oxygen consumption in low, median, and high oxygen tensions for both adults and larvae. The variations in oxygen tension resulted from the number of individuals present, the duration of the tests, and the oxygen tension of the water at the start. The same individuals were tested under these varying conditions. When the results are arranged with reference to the average oxygen tension during the experiment, it is seen that for both adults and larvae there is a strict dependence on the concentration of oxygen in the water. The values for adults varied from 31.7 ± 1.4 cu. mm. of oxygen consumed per gram-hour at an oxygen tension of between 6.3 and 5.0 cc. oxygen per liter, to 14.3 ± 2.5 cu. mm. oxygen per gram-hour at an average low oxygen tension of 2.0 cc. oxygen per liter. In the median range intermediate values were obtained. Similarly, larvae showed a variation in consumption of from 49.6 ± 2.0 to 34.0 ± 2.0 cu. mm. oxygen per gram-hour with a decrease in oxygen tension from an average low of 5.0 to one of 1.9 cc. oxygen per liter. At a median oxygen tension, the value for oxygen consumption lies in a straight line between the points established by the high and low values (Fig. 1). Similar results were found for *Desmognathus fuscus fuscus* (Table III and Fig. 1). Thus it is evident that when comparisons are to be made, the oxygen tension at which any experiments were conducted must be taken into consideration.

Winkler tests carried out with *Gyrinophilus* adults comparing groups and singles at the same oxygen tension showed no difference between the oxygen consumption of groups and singles (Table II, D). In this series the individuals at each date were tested both singly and in groups of 3 or 4. Sometimes they were tested singly first and then grouped and sometimes the reverse order was followed. In several experiments two tests were made on either the grouped or isolated individuals, which were averaged and compared with the results of an experiment in the opposite condition. On two occasions the three tests were alternated in order. The results of this series showed an average of 29.0 ± 1.0 cu. mm. oxygen per gram-hour for 12 experiments on groups of 3 or 4, as compared with 28.1 ± 1.0 cu. mm. oxygen per gram-hour for 44 experiments on the isolated individuals. The difference is not significant ($P = 0.3434$).

Similar tests with the larvae of the same species (Table II, E and F) showed no difference between grouped and isolated individuals in the case of the smaller larvae; the experiments with larger larvae indicated slightly higher oxygen consumption on the part of the grouped individuals. The difference is statistically significant. The values were, in the case of the

small larvae (2.5 grams average weight), 48.2 ± 0.8 and 48.8 ± 2.6 cu. mm. oxygen per gram-hour respectively for 5 experiments on groups of 5 individuals and for 25 experiments on the same individuals tested singly ($P. = 0.8512$). In the case of the larger larvae (4.7 grams average weight), six experiments were made on groups of 4 individuals and 20 experiments on the same isolated individuals. The average for the groups was 41.8 ± 1.2 cu. mm. oxygen per gram-hour and for the isolated individuals 34.4 ± 1.4 cu. mm. oxygen per gram-hour ($P. = 0.0362$).

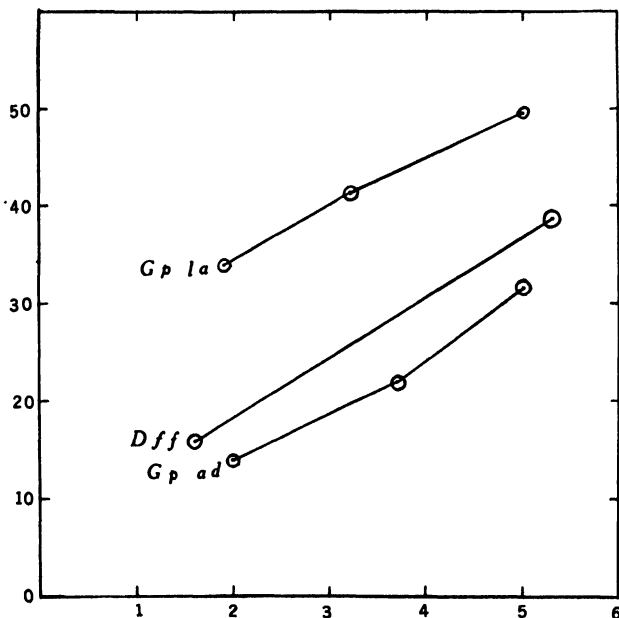


FIG. 1. Relation between oxygen consumption and oxygen tension of the water. The vertical axis represents cu. mm. oxygen consumed per gram-hour, the horizontal axis, the average oxygen tension (cc. oxygen per liter) at the end of the tests. *Gpad*, *Gpla*, *Gyrinophilus porphyriticus* adults and larvae; *Dff*, *Desmognathus fuscus fuscus*.

A consistent difference between grouped and isolated individuals which proved to be statistically significant was found in experiments on *Eurycea bislineata bislineata*. The difference does not seem to relate to any known factor other than the one tested. The groups of 4 animals consumed consistently more oxygen than the same individuals when isolated. The same results were obtained when the experiments were made on a given day first on the isolated individuals and then on the groups or vice versa, or when groups and singles were tested on a given day and the order reversed on the following day (Table II, G). The difference between the value 110.9 ± 2.2 cu. mm. oxygen per gram-hour which is the average for the group and 91.4 ± 2.0 cu. mm. oxygen per gram-hour which is the average for the

isolated individuals has a statistical significance of less than 0.0001. The actual significance seems to be in the increased activity of the group due to the disturbance of an occasional active individual while the activity of such an individual when isolated would affect only its own oxygen consumption. It is true that there was frequently an active isolated individual whose oxygen consumption during a test period was high, but it was more general for the isolated individuals to be quieter and consequently the average for the singles is low.

COMPARISONS BETWEEN SPECIES

It was hoped along with the study of aggregation effects, to ascertain whether there is any inherent species difference in oxygen consumption. Such a study is complicated by the fact that there is generally a size difference between species. The effect of size differences in oxygen consumption studies is well known and is recognized by workers on both poikilothermal and homoiothermal animals (Krogh, '16). Formulae have been advanced by various workers to reduce this difference to a minimum (Rubner, '24). As a rule oxygen consumption per unit of weight is lower for larger animals than for small ones. This indicates that the rate of respiration is more nearly proportional to surface area than to body size. However, even when results are figured according to surface area (as determined by some factor times mass), there is not a uniform value for oxygen consumption within a species when testing individuals of very different sizes (Charles, '31). Moreover, various investigators (Kayser, Le Breton and Schaeffer, '25; Wels, '25; Le Breton and Kayser, '26; Pearce, '36) have shown by studies of tissue respiration that among homoiotherms at least, pieces of tissue of equal size and surface have a higher rate of oxygen consumption when they come from smaller rather than from larger animals. This relationship holds whether the smaller animal is a young one of the same species as the larger, or belongs to a smaller species. Similar experiments with cold blooded animals have shown a decrease of oxygen consumption with increasing age and size (Hopkins, '30). Thus the higher oxygen consumption of smaller animals is a real phenomenon and not merely apparent because of their proportionately greater surface.

Tables IV and V give the values obtained at the same general temperature range for several species of salamanders. The results were obtained both by the respirometer method (Table IV) and by the Winkler method (Table V). In making up table IV only those tests were included which were made between 15.5 and 16.8° C. Results from both grouped and isolated individuals were included since no significant differences were found between these experiments. In making up table V the tests included were limited not only by temperature but by oxygen tension. Only the tests made between 15.7 and 17.2° C. and with oxygen tension not lower than 5.0 cc. per liter were included. Data from isolated individuals alone were taken, since

grouping was found to affect the results in certain cases. These same data are graphically represented in figure 2. When oxygen consumption is plotted against body weight of the animals involved, the results for different species fall, in general, on a curve established with reference to the weights of the animals, regardless of the species tested. Individuals of *Gyrinophilus porphyriticus* of widely different age and size gave values which coincided with this curve. Within the species *Desmognathus fuscus fuscus* results also correlated with the difference in size of the individuals tested. That the

TABLE IV. *Oxygen consumption in air, of four species tested at 15.5–16.8° C. Data from groups and singles combined.*

Species	Temp. °C.	Av. time each test (hrs.)	No. of tests	No. of cases	No. in group	Av. wt. (gms.)	O ₂ consumed (cu. mm./gm./hr.)	No. of values for P.E. ¹¹
<i>E. bislineata</i>	15.8–16.7	18.6	67	26	1–4	1.13	55.4±1.3	12
<i>D. f. ochrophaeus</i>	16.4–16.8	16.5	79	25	1–4	1.33	47.7±0.7	10
<i>P. cinereus</i>	15.5–16.0	13.6	204	30	1–4	0.98	41.4±0.8	10
<i>D. f. fuscus</i>	16.2–16.8	14.1	123	38	1–4	2.50	39.0±1.3	16
<i>G. porphyriticus</i>	15.8–16.7	8.4	37	15	1–2	12.1	17.6±0.6	8

¹¹ P.E. = Probable error.

TABLE V. *Oxygen consumption in water, of four species tested at 15.7°–17.2° C.; lowest oxygen tension at end, 5.0 cc. per l. Data from isolated individuals alone.*

Species	Temp. °C.	Time (hrs.)	No. of tests	O ₂ tension (cc. O ₂ /l.)		Av. wt. (gms.)	O ₂ consumed (cu. mm./gm./hr.)	No. of values for P.E. ¹¹
				at start	av. at end			
<i>E. bislineata</i>	16.0–16.5	2	48	6.5	5.9	1.24	89.0±0.7	7
<i>D. f. fuscus</i>	16.5–17.0	2	20	6.1	5.4	1.88	59.7±3.8	4
<i>D. f. ochrophaeus</i>	17.0	2	28	6.0	5.5	1.49	55.8±2.7	5
<i>G. porphyriticus</i> larvae	16.5–17.0	2	25	6.3	5.7	2.5	48.8±2.6	5
<i>D. f. fuscus</i>	17.0–17.2	2	40	6.3	5.4	2.94	51.1±1.3	7
<i>D. f. fuscus</i>	16.0–17.0	2	6	6.3	5.3	4.4	38.8±1.8	6
<i>G. porphyriticus</i> larvae	15.7–17.0	1.7	24	6.2	5.3	4.5	40.8±2.6	5
<i>G. porphyriticus</i> adult ¹²	17.0–17.5	2	6	6.2	4.6	4.5	45.6±2.4	6
<i>G. porphyriticus</i> adults	16.0–17.0	1	50	6.4	5.3	12.7	28.9±1.1	11

¹² Oxygen tension went a little below 5.0 cc. per l.

rate of oxygen consumption per unit of weight is as much a matter of actual size as of age is evident from the fact that the largest (oldest) individuals of the smaller species fall in line with the smallest (youngest) individuals of the larger species in this respect. This is in accord with the results of tissue respiration studies reported above. It is interesting to note that the curve for oxygen consumption in the medium of moist air is lower than that for the aquatic medium. A comparison of the two types of tests is justifiable in view of Wilder's ('37) careful analysis of the two methods.

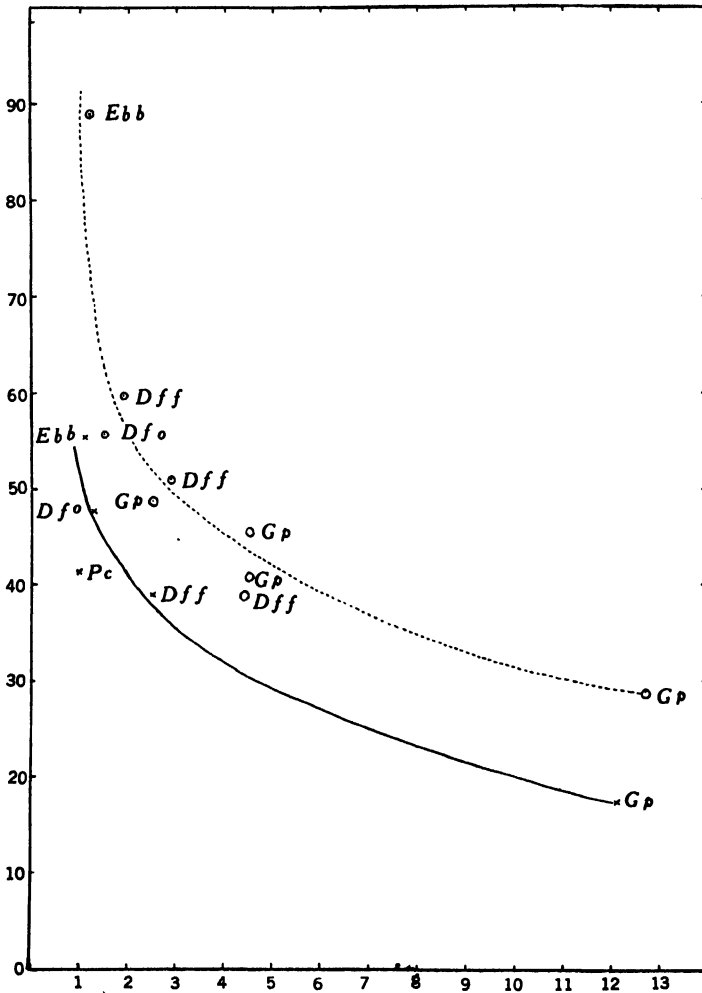


FIG. 2. Oxygen consumption of species of salamanders plotted with reference to body weight. The vertical axis represents cu. mm. oxygen consumed per gram-hour, the horizontal axis, body weight in grams. Winkler tests of aquatic respiration shown by circles and dotted line; respirometer tests of aerial respiration shown by crosses and solid line. *Gp*, *Gyrinophilus porphyriticus*; *Dff*, *Desmognathus fuscus fuscus*; *Dfo*, *Desmognathus fuscus ochrophæus*; *Ebb*, *Eurycea bislineata bislineata*; *Pc*, *Plethodon cinereus*.

In Wilder's similar comparison between aquatic and aerial respiration, the difference was statistically insignificant. Our results with the species tested by the two different methods is given in table VI and here, the larger series now available indicates statistical significance for the difference between oxygen consumption in air and in water for three of the four species. It is true that the duration of the experimental period was longer in the respirometer

than in the Winkler tests, which might partially account for the lower metabolic rate shown by the former. It is equally true, however, that the *Desmognathus* and *Eurycea* species, while found in the vicinity of creek beds, more often remain quietly in moist air under cover of stones and logs at the water's edge, than directly in the water. It is reasonable to suppose that such being the case, metabolism tests in moist air would reveal more nearly their normal respiration than tests made in a medium into which these salamanders are accustomed to dash for means of escape, but in which they do not naturally rest for extended periods of time. *Gyrinophilus* adults are frequently found in and along streams, but they also wander over the land in the neighborhood

TABLE VI. *Statistical comparison between oxygen consumption in air and in water (Data in Tables IV and V).*

Species	O ₂ consumed (cu. mm./gm /hr.)		Diff.	P.E. of Diff. ¹³	Diff. P.E.
	In air	In water			
<i>G. porphyriticus</i> adults	17.6±0.6	28.9±1.1	11.3	1.25	9.0
<i>D. f. fuscus</i>	39.0±1.3	51.1±1.3	12.1	1.84	6.6
<i>D. f. ochrophaeus</i>	47.7±0.7	55.8±2.7	8.1	2.78	2.9
<i>E. bislineata</i>	55.4±1.3	89.0±0.7	33.6	1.48	22.6

TABLE VII. *Statistical comparison between species of the same general size. A. Tests made in air (Data in Table IV).*

Comparison	Diff. (cu. mm. O ₂ per gm./hr.)	P.E. of Diff. ¹³	Diff. P.E.
<i>E. bislineata</i> : <i>D. f. ochrophaeus</i>	7.7	1.48	5.2
<i>D. f. ochrophaeus</i> : <i>P. cinereus</i>	6.3	1.06	5.9
<i>E. bislineata</i> : <i>P. cinereus</i>	14.0	1.53	9.2

B. Tests made in water (Data in Table V).

<i>E. bislineata</i> : <i>D. f. fuscus</i>	29.3	3.86	7.6
<i>D. f. fuscus</i> : <i>D. f. ochrophaeus</i>	3.9	4.65	0.8
<i>E. bislineata</i> : <i>D. f. ochrophaeus</i>	33.2	2.78	11.9

of streams and are doubtless at home in both aquatic and terrestrial situations. *Plethodon* species, on the other hand, are never found in streams, but are entirely terrestrial in their habits. Accordingly, no Winkler tests were made on this species, since these tests would place the animals in unnatural conditions and be of little value in determining their normal respiration.

For three species a comparison is possible between the aërial respiration of individuals of nearly the same size (Table VII, A). Such a comparison indicates differences in oxygen consumption which are statistically significant

¹³ A difference of less than 3 times the probable error of the difference is not considered statistically significant.

and which seem to relate to the general behavior characteristics of the species rather more than to their size. If the amount of oxygen consumed per gram per hour were entirely a matter of size, we should expect *Eurycea bislineata bislineata*, *Desmognathus fuscus ochrophacus* and *Plethodon cinereus* (average weights 1.13 grams, 1.33 grams and 0.98 gram respectively) to give much closer results. The results for *Plethodon cinereus*, particularly, do not fall in line with the curve for oxygen consumption as related to body weight. Between *Plethodon cinereus* and *Eurycea bislineata* there is a wide difference in oxygen consumption. The former is a very slow sluggish species and the latter a very lively one. The habits of *Desmognathus fuscus ochrophacus* are intermediate between the two with respect to activity, and the value for its oxygen consumption lies correspondingly between the values for the other two.

Similar correlations may be pointed out between the oxygen consumption and activity of *Eurycea bislineata bislineata* (average weight 1.24 grams) and two subspecies of *Desmognathus*, *D. fuscus fuscus* (average weight 1.88 grams) and *D. fuscus ochrophaeus* (average weight 1.49 grams), when their aquatic respiration was tested (Table VII, B). *Eurycea bislineata* as the most active species gave very high results, significantly higher than results for the other two species. A comparison between individuals of similar size of the two closely related subspecies, *Desmognathus fuscus fuscus* and *Desmognathus fuscus ochrophaeus*, indicates a slightly higher oxygen consumption for *D. fuscus fuscus*, but the difference is not statistically significant. The slight difference, however, offers an interesting lead for further work. With a larger number of cases it would not be surprising to find a significant difference in view of the relative difficulty in collecting the two subspecies. *D. fuscus fuscus* is faster when escaping than *D. fuscus ochrophaeus* and is in general a more active subspecies. Both subspecies are found in the same stream beds in Ohio and northwestern Pennsylvania. *D. fuscus ochrophaeus* is also found farther from stream beds under stones and logs in moist forests. A discussion of the evolutionary and ecological relationships of these two subspecies is given by Dunn ('26). Speculation as to whether the wider ranging local distribution of *D. f. ochrophaeus* is related to its oxygen requirements or not, must wait until the relations in oxygen consumption between this subspecies and *D. f. fuscus* have been definitely established. It is possible that an ability to resist drying may be the significant factor accounting for its appearance as a terrestrial form.

DISCUSSION

Physiological processes are affected by the physiological state of the animals concerned; as well as by a variety of environmental factors, and it is not surprising to find considerable variability in the rate of respiration of animals tested under conditions as uniform as possible. In frogs, heat production has been found to drop off quite rapidly with the cessation of feeding and to

decline gradually to a constant level (Hill, '11). Smith ('35) has pointed out the decline in oxygen consumption of the lung-fish that occurs during fasting. For the present experiments, time was allowed for the first rapid decline before making the tests. Tests were usually made from a week to 10 days following the last feeding. In making comparisons between individuals the time since collection could not be kept constant. There are indications that even in animals which have been kept in a feeding condition in the laboratory, there is a certain acclimatization to laboratory conditions. No data on this point can be presented at this time, but it is believed that the physiological states of the animals are not comparable after widely different intervals since collection. Tests were confined in so far as was possible to animals which had been in captivity for not more than four months. Efforts were made to do as many experiments as possible in the first weeks following collection in an attempt to test the "normal" respiration.

Obviously, activity speeds up heat production and rate of respiration and tests to be comparable must be made on animals in a quiet, resting condition. During the long-period tests the animals showed little movement and would remain for hours in the same position. During the shorter tests of one or two hours the animals were usually quiet, although occasional movements were observed. It is felt that it is permissible to make comparisons between species in such cases on the grounds that the amount of activity itself is a species characteristic and as such should be measured. And even if there were no movement during a test, activity and struggle during the capture previous to the tests might affect the respiration for some time following the time at which movement ceased. Such a condition has been reported by Benedict ('32) for reptiles.

Concerning the fact that no uniform difference was observed between the oxygen consumption of grouped and isolated individuals except in one or two cases, it is interesting to note that the most striking case was found with the most active species, where movements of one individual in a group would arouse the others to activity, whereas occasional movements of an isolated individual would have no effect on the other isolated individuals. Since the salamanders do not naturally cluster together in the aquatic medium the increased muscular activity caused by the proximity of other animals is not surprising. This is just the opposite result from that reported by Clausen ('36) for reptiles. Working with *Storeria dekayi* he found that individual snakes when aggregated consumed less oxygen than when isolated. These snakes belong to a species which aggregates in nature, particularly in winter, and the presence of the group evidently has a quieting effect on their activity and their resultant metabolism. Similarly a lowering of oxygen consumption has been found in brittle starfishes (*Ophioderma brevispina*) when aggregated (Allee, '27). In this case a lowering was also found when glass rods were provided for the brittle stars to twine around, which would indicate that

the effect of the group was less a social than a mechanical phenomenon. While salamanders do frequently cluster together when kept in the laboratory, perhaps as a thigmotactic response, the result of clustering evidently does not seem to be one of lowered rate of respiration. Perhaps the isolated individuals that were tested satisfied this thigmotaxis in the respirometers by crawling up into the top of the bell. They were frequently found in this region, or even with their heads pressed up into the entrance to the manometer tube. Even among the grouped individuals they were as often found singly up under the top of the bell, as clumped together.

The lowered rate of oxygen consumption found with the early tests of grouped individuals of *Desmognathus fuscus fuscus* and *D. fuscus ochrophaeus* seems definitely to be a matter of sensitivity to reduced oxygen tension, since no difference was found when provision was made for keeping the oxygen tension the same for the grouped and isolated individuals. This is the more interesting in that Hyman ('29, '32), has reviewed the literature dealing with the effect of oxygen tension on oxygen consumption and states that the vertebrates in general (fish) consumed oxygen at a constant rate, regardless of the oxygen content of the medium down to rather low tensions. Among invertebrates no uniformity exists. Even among closely related species of insects the aquatic nymphs vary in their ability to remove oxygen from water at decreased oxygen tensions (Fox, Wingfield and Simmonds, '37). While there seems to be some adaptive significance in the fact that one species which is accustomed to live in still water, can consume oxygen at the same rate to greatly lowered oxygen tensions, while certain forms from rapid water show an almost linear relationship between oxygen consumption and oxygen tension, the correlation is not perfect since another slow water form does not show this ability. Apparently fishes are more variable in this respect than was first thought. Hall ('29, '30) found certain marine species rather sensitive to decreased oxygen content. In the case of fishes the necessity of differentiating between an effect which may be due to carbon dioxide and one due to low oxygen has been pointed out by Wells ('35). Powers, *et al.* ('32) have shown that the carbon dioxide effect may be independent of low oxygen. Among Amphibia, Dakin and Dakin ('25) reported that axolotls are independent of the oxygen pressure which may fall considerably until a certain minimum (not stated) is reached before the oxygen consumption of the animals per hour is affected. No data were given. An extensive series of experiments reported by Helff and Stubblefield ('31) on *Rana pipiens* tadpoles demonstrated remarkable respiratory regulation throughout considerable ranges of oxygen tension. One may point out that in their natural habitat tadpoles find it necessary to take refuge in the mud and leaves at the bottom of quiet ponds where the oxygen supply must frequently be low. The ability to remove oxygen from such water at the same rate as from more highly oxygenated water is obviously advantageous. In view of these conflicting

results within the Amphibia it seems advisable to make no generalizations even for the family Plethodontidae. But, among the plethodontid salamanders tested, there is little doubt that the ability of the animals to remove dissolved oxygen from the water depends on the concentration of oxygen in the water, and that they are sensitive even to small changes in oxygen tension. Such has been found the case for three different species, and in one, not only for adults but for larvae with well developed external gills.

Differences between oxygen consumption for three of the species studied here have been reported by Wilder ('37), but comparisons were not made between individuals of the same size. It seems advisable to emphasize the importance of size and its relation to oxygen consumption per unit of weight. It is common knowledge that larger animals, even within a species, have a lower rate of oxygen consumption per unit of weight than small animals. This has been found to be the case also with the salamanders, and the fact precludes comparisons between oxygen consumption of different species (per unit of weight) unless comparisons are made between individuals of similar sizes. Such comparisons made between the species reported here do indicate species differences in oxygen consumption which correlate with the relative activity of the species tested. It would be interesting to make similar tests on anesthetized individuals to see whether these species differences were actually metabolic differences irrespective of the degree of activity or whether they are entirely the result of and directly proportional to the number of movements made during a given test. Bernhardt ('34) has studied the effect of chlorotone on oxygen consumption of *Rana clamitans* tadpoles and noted a depressing effect of solutions below the concentration at which anesthesia is produced. It is possible that different species might present different sensitivities to chlorotone and so defeat the purpose of such tests. Species differences in oxygen consumption for several species of *Ambystoma* larvae of the same age and size have been reported by Helff ('27). He noted that the species showing the least tendency to activity during the tests had the highest rate of oxygen consumption, thus emphasizing the metabolic differences inherent with the species. Helff did not draw any conclusions as to the ecological relationships of the forms studied, but Noble ('31) has pointed out that, among these species of salamanders, the lowest rate of oxygen consumption was found with the form which is most aquatic as an adult. This is the opposite of our findings with plethodontid salamanders, although the conditions are somewhat different since Helff's tests were all on aquatic larval forms.

Correlations between habitat and metabolism have been found for certain species of mayfly nymphs, caddis larvae and isopods (Fox and Simmonds, '33, Fox, *et al.*, '35). It was shown that the forms which inhabit swiftly flowing streams have a higher oxygen consumption than closely related species from still waters or slow streams. It has also been shown (Washbourn,

'36) that oxygen consumption of trout fry reared in swiftly flowing water is greater than that of fry reared in slow water, though why this should be so is not evident. The explanation may lie in the adaptive changes that take place in the alkali reserve and the number of red blood corpuscles in fish blood in response to changes in the carbon dioxide and oxygen tensions of the surrounding medium (Powers, *et al.*, '32, Powers, '34). It is doubtful whether oxygen requirements have been directly responsible for choice of habitat among different species. While "physiological species differences" are conceivably as reliable as anatomical and behavior differences, it would be difficult to say whether a physiological difference was the result or the cause of such a thing as habitat "preference." There can be no harm, however, in noting a correlation between the fact that the more active salamander species such as *Eurycea bislineata bislineata* and *Desmognathus fuscus fuscus* live in and about the water's edge, and that the less active species *Desmognathus fuscus ochrophaeus* is more terrestrial, while the very sluggish *Plethodon cinereus* is entirely terrestrial in habits, and that as the habits become more terrestrial, the rate of oxygen consumption decreases. These facts suggest the possibility that the habitat selection of a species of salamanders may be indirectly related to its oxygen requirements. Perhaps a less active species can live in drier situations where buccopharyngeal respiration and a limited amount of cutaneous respiration may provide sufficiently for its oxygen needs; while the livelier species must live in and about water so that more extensive cutaneous respiration, made possible by the moist skin, can provide for the greater oxygen demand.

SUMMARY AND CONCLUSIONS

The oxygen consumption per gram per hour of several species of plethodontid salamanders in air and in water was determined by the respirometer method and by the Winkler method respectively. It has been demonstrated that results obtained by these two methods are comparable (Wilder, '37).

There was no significant difference when salamanders were tested singly or in groups of 3 or 4, when oxygen consumption *in air* was determined. The species tested were *Desmognathus fuscus fuscus*, *Desmognathus fuscus ochrophaeus*, *Eurycea bislineata bislineata* and *Plethodon cinereus*. Similar comparisons between paired and isolated individuals of *Gyrinophilus porphyriticus* also showed no difference.

When *D. fuscus fuscus* and *D. fuscus ochrophaeus* were tested *in water* there was less oxygen consumed per gram per hour by the grouped than by the isolated individuals when they were tested for the same length of time and in the same sized containers. The oxygen tension was lowered further in the case of the groups than for the singles. When experiments were devised to eliminate this difference, the difference in oxygen consumption also disappeared. Similar tests (in water, at uniform oxygen tension) of *Gyri-*

nophilus adults likewise showed no difference between the oxygen consumption of groups of 3 or 4, and the same individuals tested singly. Experiments with *Gyrinophilus larvae* did not give consistent results. In one series, the groups showed a higher rate of oxygen consumption than the isolated individuals, and in another series, no difference was found. *Eurycea bislineata bislineata* tested singly and in groups of 4 showed a consistently higher rate of oxygen consumption in water when grouped, probably due to the disturbance of the groups by the activity of one individual.

The oxygen consumption of *G. porphyriticus* adults and larvae and of *D. fuscus fuscus* adults was shown to be dependent on the oxygen tension of the water in which they were tested. The dependence on slight lowering of the oxygen tension of the water is advanced as the explanation for the lower rate of oxygen consumption of the groups of *D. fuscus fuscus* and *D. fuscus ochrophaeus* as first tested.

A comparison is made between the rate of oxygen consumption in various species tested in air and in water at the same temperatures, and (in the case of the tests in water) at the same oxygen tension. In every case oxygen consumption in water was higher than in air. By plotting the oxygen consumption of the different species and individuals within a species, with reference to their body weight, the inverse relationship between oxygen consumption and body weight is demonstrated. It is evident that species differences in oxygen consumption when calculated per gram per hour cannot be recognized on the basis of comparisons made between species of different sizes.

Species differences may be recognized between similar sized individuals of different species. Such differences in general correlate with the normal activity of the species. When tested *in air*, *Plethodon cinereus* had the lowest rate of oxygen consumption and *Eurycea bislineata bislineata* the highest. *Desmognathus fuscus ochrophaeus* was intermediate. Of these three species, *Plethodon cinereus* is the least active and *E. bislineata bislineata* the most active.

Tests *in water* demonstrated a similar correlated difference between the two *Desmognathus* subspecies (*D. fuscus ochrophaeus* and *D. fuscus fuscus*) and *E. bislineata bislineata*. The latter, the most active species, again showed the highest rate of oxygen consumption.

A further correlation was pointed out between the normal habits of these species and their activity and resultant rate of oxygen consumption. The most terrestrial species are the least active and have the lowest rate of oxygen consumption, and the most aquatic species (of those tested) are the most active, and their oxygen consumption is the highest.

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REVIEWS

USEFUL TREES AND SHRUBS ¹

A reference work on useful trees and shrubs has been prepared by the assistant professor in landscape architecture of the University of Illinois, in the unusual form of a card file, giving data on approximately 500 hardy woody plants in common use as ornamentals. The Preface states that "The data presented in this card file is average over the northern states and Canada, and has been checked against the printed observations of many authorities." The cards are filed alphabetically by the Latin names of the genera, and for each species give the native habitat, hardiness, size, form, color, season of foliage, flower, and fruit, cleanliness, aspect and value, and ecological "association." At the right of each card are blank spaces for summer and winter sketches. The cards measure 4 by 6 inches. White cards are for deciduous trees, canary for deciduous shrubs, green for conifers, salmon for broad-leaved evergreens, and cherry for vines. "The nomenclature follows Standardized Plant Names in accord with nursery practice—necessary and practical for those who wish to buy plants." There is a bibliography of about 42 titles.

C. STUART GAGER

BROOKLYN BOTANIC GARDEN

PLANT PHYSIOLOGY ¹

This college text contains much material that is ecological or on the borderline of ecology and plant physiology. For example, chapter III deals with "The Soil," with paragraphs on soil water, soil atmosphere, soil temperature, soil organisms, and several very effective pages on conservation and the destruction of soil fertility through lumbering for immediate profit without regard to the ultimate disastrous results. Chapter XXIV deals with "Plant Associations" (10 pages), chapter XXV with "Environment" (18 pages).

Dr. Seifriz's text is throughout so admirable that one hesitates to question the accuracy of his interpretation of the classic experiment reported in 1727 by Stephen Hales in his *Vegetable Staticks*, and which Dr. Seifriz cites as illustrating Hales's experiments in "root pressure," with which he states, "Plant physiology had its beginning." The quotation on pages 5 and 6 of

¹ Robinson, Florence Bell. 1938. Useful trees and shrubs. *The Gerard Press, Champaign, Illinois*. \$4.50.

¹ Seifriz, William. 1938. The physiology of plants. 315 p. 95 fig. *John Wiley and Sons. New York*. \$3.50.

Seifríz is from chapter II, pages 77 and 78, of *Vegetable Statics*; and the illustration (Fig. 1 of Seifríz) is "Fig. 10" of Hales, facing page 88. Hales states that his purpose is "to inquire with what force they [i.e., 'Vegetables,' not roots] do imbibe moisture," and in his "Experiment XXVIII" (p. 90) he modifies Experiment XXI by stripping off the leaves and records that while the mercury in the glass tube attached to the stem rose 2.5 inches (as against 8 inches with the leaves on) "it soon subsided *for want of plentiful perspiration of the leaves.*" Clearly Hales's experiment demonstrated the so-called "lifting power of transpiration," not root pressure.

It is in his chapter III that Hales investigates root pressure. He says (p. 100): "Having in the first chapter shown many instances of the great quantity imbibed, and perspired by trees, and in the second chapter seen the force with which they [i.e., 'trees,' not roots] do imbibe moisture. I propose next to give an account of those Experiments, which prove with what great force the sap of the Vine is pushed forth, in the bleeding season."

Then follows "Experiment XXXIV" (p. 101), with the conclusion: "From this Experiment we find considerable energy *in the root* [italics the reviewer's] to push up sap in the bleeding season." This experiment is illustrated by Hales's Fig. 17 (facing p. 106), which, in all essentials, is the same as Fig. 29, "a simple manometer for demonstrating root pressure," on page 78 of Seifríz. Hales's figure (Fig. 1 in Seifríz) is, in all essentials, the same as Seifríz's Fig. 28 A, "Rise of mercury column due to transpiration from leaf surfaces."

C. STUART GAGER

BROOKLYN BOTANIC GARDEN

PROBLEMS IN ANIMAL ECOLOGY¹

Dr. Bodenheimer was originally trained under Professor Richard Hesse in Germany and has been located now for several years at the University of Jerusalem where he has been active in the study of the ecology of Palestinian animals. He displays a freshness of point of view in the present small volume which is not the least attractive feature of a stimulating discussion.

The book emphasizes a tendency toward a new orientation in animal ecology which has been developing for some years. From several different lines of approach and in various countries, scholars have been realizing more and more that populations of animals offer a fertile field for ecological exploration both in nature and in the laboratory. Probably it will surprise some ecologists more than it does Professor Raymond Pearl to find that with this newer orientation, Pearl takes place along with Moebius, Shelford, Hesse, Peterson and others of the well-thumbed list as a pioneer in ecology.

A careful reading and some study of the present book emphasizes the accuracy of the author's summary of its contents, which is given in the preface.

¹ Bodenheimer, F. S. 1938. *Problems of Animal Ecology*. Oxford University Press. vi + 183 pp. \$4.00.

Dr. Bodenheimer says that he is dealing with certain problems of animal ecology which have been somewhat neglected in summarizing books. He contrasts physiological with ecological longevity and quotes with approval an earlier statement that "the life-history of the individual species will always remain the basis of animal ecology."

Perhaps as an outgrowth of his experiences in Palestine, economic applications are evidently much in the mind of the author. From such contacts he has found that "the ecological interpretation of the life-history has passed its primitive stages and is a valuable instrument of prognosis." In one of the most detailed chapters, there is a serious attempt to supply some badly needed knowledge concerning the interrelations of early stages of development during the growth of a population. In this connection, extensive original data are presented concerning the population growth of a Palestinian strain of *Drosophila*. Here at times, notably on p. 58, the publication of experimental results in book form seems premature. Even so, this is a strong section of the book.

In discussing the problem of so-called biological equilibrium, some attempt is made to synthesize a general point of view from (a) the climatic school, (b) the biological school, and (c) the school of mathematical analysis. The treatment of the basic data and the claims of the school of biological control is especially critical.

Animal communities are regarded as "valuable statistical units for descriptive and classification purposes" but "the presence of high integrations to super-organismic structures in animal communities has not so far been proven." And again: "It does not seem just to conclude from the mere maintenance of the food pyramid within any biocoenosis that intrinsic regulations occur within the community."

The final chapter is devoted to "the interaction of environment and heredity within the organism as demonstrated by the phenomenon of diapause, sex-determination, geographic variation, and adaptation." The sound thesis presented is that the understanding of these processes "necessitates a close cooperation between genetical and ecological biology." The author's personal approach can be judged from the following quotations from the last page of the book:

"As long as such important branches of biology as ecology, zoogeography, comparative anatomy, palaeontology, taxonomy and experimental morphology are forced to declare that, following their own methods, some kind of Lamarckian theory is 'probably the only intelligible theory of a natural evolutionary process ever advanced' it is the duty of every geneticist to reconsider the limitations of his present methods. . . ." The book closes with a disclaimer of the intention of presenting a pre-Lamarckian essay but does plead for a "fully unprejudiced approach to the problem as opposed to the *a priori* orthodox attitude of a large majority of present-day biologists."

The preface states correctly: "The book is no easy reading." There is much documentation but this weight does not produce the difficulty in reading. Neither does it come from the nature of the subject matter. The chief difficulty seems to be caused by the great condensation in presentation. At times the statements narrowly escape being cryptic. This is especially the case with the legends for the numerous diagrams and with the tabular material and unfortunately frequently extends to the discussion of figures and tables in the text (*e.g.* pp. 94-95). Many of the tables are composed of mean values only and throughout there is no indication of the statistical significance of these means. The book closes with 238 skeletonized citations to original sources and a topical index.

Dr. Bodenheimer is to be congratulated warmly for having produced the present book. Considering the probable audience, it is of relatively little importance that the conclusions reached seem to waver at times under the impact of conflicting data and opinions. This is distinctly not a book for beginners, but all teachers and research workers in ecology and directors of investigations concerning insect pests and other applied aspects of ecology, will be well advised to become familiar with its contents.

An important difficulty is one over which the author had no control. Even after making allowance for the full and attractive type-page, the many tables and diagrams and the sturdy manufacture, like so many other books printed in England and offered for sale in the U. S. A., the price is altogether too high. The price of 2.16 cents per page cannot be wholly justified by the existing tariff charges, though these are indefensible when applied to books at this intellectual level.

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BOOK NOTICES

University of Oxford, Department of Forestry. 1938. Forest Bibliography to December 31st. Part III. 201-274. *Oxford University Press.* 12s. 6d. Continuing this useful publication, previously reviewed (*Ecology* 19: 158-159. 1938), this part contains citations of literature dealing with forest protection from man, animals, atmospheric factors, fire, weeds, and other agencies.

L'Institut des Parcs Nationaux du Congo Belge. 1937. Aspects de Végétation des Parcs Nationaux du Congo Belge. 1 (1-2): 12 pl. This publication is to appear in fascicles of six plates each, accompanied by explanatory notes. The publication will be issued in series, each devoted to one of the national parks. The first series has just been received for review (October, 1938), and concerns the Parc National Albert. The beautiful illustrations, in phototype, of aspects of vegetation should be of much interest to ecologists. The title is "Aperçu général de la végétation," and the author is W. Robyns, director of the Jardin Botanique de l'État, at Brussels. It is announced that the publication will not be sent in exchange.

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NOTES AND COMMENT

CHANGES OBSERVED IN THE MAMMAL FAUNA OF BARRO COLORADO ISLAND, 1929-1937

More than three hundred papers have been published on the flora and fauna of Barro Colorado Island making it the best known area in tropical America. Since it is so well known and is visited by many biologists a record of the changes in the mammal fauna observed between 1929 and 1937 may prove useful to other workers. Barro Colorado Island is a biological preserve located in Gatun Lake, Panama Canal Zone, under the direction of the Institute for Research in Tropical America. For details of its flora and fauna reference should be made to the bibliographies published in the annual reports. A summary of our knowledge of the mammals and their life histories is found in a previous paper (Enders, '35).

My first attempt to determine the numbers of the many species of mammals on the Island was made June to August, 1929. Studies of the mammals were continued in '30, '31, '32, '33, '34, '35, and '37. A total of approximately fifteen months was spent on the island during these years extending through all months excepting late September and October. Extensive notes were kept on when, where, and how many mammals were observed. During August and September, 1937, a special effort was made to determine what changes in the mammal fauna could be detected. It is with pleasure that I acknowledge the help of O. P. Pearson, Samuel Cresson and Ratibor Hartman.

This work was part of a program of study sponsored by the Academy of Natural Sciences and Swarthmore College with the support of a grant from the American Philosophical Society.

METHODS

During the study much of the Island was covered by trail and several trips into the less accessible parts made without benefit of trails. The long inlets or esteros were examined from dugouts. Previous experience had demonstrated that more mammals were seen in the morning and at and after dusk so most of the observations were made at these hours. At this time of the year the ground is fairly clear of leaves and the clay is soft enough to record footprints which are invaluable in the study of the larger mammals. No traps were used hence few observations were made on the smaller rodents. The party consisted of two men who had had three months experience in tropical collecting, a sixteen year old boy of German-Indian parentage who had spent his entire life in the tropical forest, and the writer. We operated together as one party until we were sure of our methods then we worked either in twos or singly as circumstance dictated. Each man or party noted the time spent in the forest, the trails or area covered, the species and number of mammals observed and the exact location where observations were made, noted tracks and diggings, in short, recorded all evidences of the presence of mammals. These records have been compared with similar records made in previous years.

The validity of my conclusions rest, therefore, not upon a solid quantitative basis, but upon no better basis than a familiarity with the area and its inhabitants: familiarity gained over a period of eight years and reenforced by extensive notes and frequent estimates made during the past eight years.

RESULTS

Profound changes have occurred in the relative abundance of various species since 1932. The large mammals have diminished in numbers while the smaller ones have increased. The outstanding surprise, next to the decrease in the numbers of large carnivores, was the slight change of population about the laboratory area.

Of the larger carnivores the tayra has held its own or increased slightly. Several were seen and tracks noted in April and August 1937. Although the tayra eats a great deal of fruit no doubt it also benefits from the abundance of rodents that has followed the decrease of the puma and ocelot. In 1932 I placed the ocelot population of the Island at 12. Since that time "sign" has disappeared from Orchid Island, the rear light on Miller Trail, from the Almendro (SM1) as well as from all places where "sign" was previously seen, excepting Fuertes House and near the laboratory. Hours on the trails disclosed but one track and that at Snyder-Molino 5. Four ocelots is a generous estimate now. The puma population is more difficult to judge but the absence of tracks or "sign" in such favored regions of Zetek 11 and Drayton Trail leads me to the conclusion that the puma is now comparatively rare on the Island and has dropped dangerously low for survival.

Carpenter records an increasing population of howling monkeys. His figures are very accurate being based on actual count. Even casual observation indicates that clans are more numerous; that the territory occupied by howlers is more extensive as the trees in the forest toward Barbour Point grow taller. The white face monkey holds its own or is increasing while the titi or squirrel monkey appears to be increasing. *Aotus*, the night monkey, is seen as frequently as before.

The agouti and paca have increased in numbers, more apparently, than any other mammals excepting the armadillo. Agouti could be seen at any hour of the day on most of the trails. The bareness of the ground was responsible for the ease with which terrestrial mammals could be observed but there was no mistaking their increased numbers. Paca, too, have increased although the increase seemed to be chiefly along streams away from the trails in the more remote portions of the Island. While formerly abundant at Zetek 11 no signs were found there during this investigation. Small rodents were seen from time to time very much to the astonishment of our young hunter who, in many years of night hunting, had not seen many small rodents.

The collared peccary has become less and less common since 1932. Aside from the band or bands near the laboratory clearing they were difficult to locate in 1935 while in 1937 only 6 bands were located. The laboratory band was still about ranging rather widely for food, a band was living near Drayton, another on Miller Trail where, in 1932, no less than three bands were observed, another at the junction of Donato-Barbour Trails, a band between 10 and 19 on Armour Trail and one on the estero beyond Point Salud. From the rest of the trails and much of the Island signs of peccary have disappeared. Reproduction is going on as young were seen and their tracks noted on several occasions.

White-tailed deer are either holding their own or are more abundant about the center of the Island. The small brocket deer has increased in the same areas where the paca has increased, namely, the remote portions of the Island not traversed by trail. A few are now found along Barbour.

Tapir tracks or tapir "signs" were much less abundant in 1937 than before. Tracks were seen at Drayton 16 and near Nemesia. Many of the esteros where tracks were conspicuous in 1932 show no signs of tapir, old wallows are deserted and only two dung deposits were found. The numbers of tapir are low, possibly as low as two.

Tamandua, the three-toed anteater, has increased in numbers. Observation indicates that they were seen four times as often in 1937 as in 1930-1932. The increase in the number of nine-banded armadillo is even more striking. They were seen both in

daytime and at night, and their digging was much in evidence. Having seen but one in 1929-1935 it was a surprise to see several each day in 1937.

DISCUSSION

What then has led to the changes in population? It is my belief that conditions were normal up to 1932. Since that time more and more hunting has been going on over the portions of the island far from the laboratory. That poaching goes on is evident from the reports of guns which we have heard, from tracks and from encounters with poachers. They shoot the bigger cats, peccaries, and tapir. It is these animals that are decreasing in numbers while those that are not hunted increase. Since hunting is done both day and night all these species are killed. Hunting is usually done along the well established trails although some pickets have been cut through good hunting territory and some shooting is done from cayucos. The mammal population about the laboratory is practically unaffected since poachers avoid this area.

An island fauna is helpless under prosecution. On the mainland, even in remote regions, game will move out of a territory when hunted, returning later when things are quiet. This is not possible on Barro Colorado. Such individuals as seek the mainland would be shot before becoming established so would never return. This inability to move into other territory, plus the number of hunters, brings the numbers of these hunted species down to a dangerous level.

The large numbers of mammals on Barro Colorado Island has been ascribed to the filling of Gatun Lake which was supposed to have forced mammals out of the lowlands onto the Island. Chapman ('29, p. 5) questions this explanation. In referring to this problem the writer (Enders, '35, p. 389) has said "An unnatural concentration forced upon a fauna from 1910 to 1914 would not persist in 1932. There is, broadly speaking, no sign of a diminution of the number of mammals." In 1932 the population while not stable was approximating the aysruptole. It is even less probable that the smaller population of mammals observed in 1935 and 1937 could be traced to the lessening of the effect of this early concentration.

SUMMARY

Coati, kinkajou, squirrel monkey, appear to be holding their own as is *Didelphis*.

The puma and ocelot have decreased in numbers as have the collared and white-lipped peccary and the tapir. Monkeys show an increase but the most marked increase is in the terrestrial rodents and the armadillo.

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AN ECOLOGICAL NOTE ON THE BROOK LAMPREY

The writer has spent considerable time during the past nine years studying the characteristics, reactions, and habits of the brook lamprey (*Lampræta lamottenii* (Le-Sueur)).

Located about one mile south of Morgantown, W. Va., there is a small stream, locally known as Cobun Run, which empties into the Monongahela River. Numerous specimens have been taken for various scientific studies from time to time from this stream.

Until the summer of 1931 no difficulty was experienced in locating the larval forms. It was only necessary to dig into the mud banks containing decaying organic matter along the edge of the stream and usually at numerous points several larvae would be taken with each shovelful of mud removed. At no time were any larvae observed swimming in the water.

After an absence of several weeks the writer visited several of the points from which he had previously taken specimens and found the stream to be dry except for some pools in the deeper portions of its bed. Digging in the usual places failed to reveal any larvae even though the mud was still rather moist.

After going upstream some distance a pool was reached which was literally swarming with larvae of all sizes. Through the course of the stream three such pools were found. Digging in the mud banks at the edges of these pools failed to reveal a single animal.

A careful check was kept on these pools during the remainder of the dry period which lasted for approximately another three weeks. The lampreys remained in a free swimming state until the stream was filled and the water began to flow in it again. They then left the water and buried themselves in the mud again.

The animals were evidently prevented from going downstream about one-half a mile to the river because of the pollution at the mouth of the stream due to the presence of oil.

Since 1931 no more specimens have been located at the points where they were originally taken but have been rather plentiful along the edges and in the bottoms of the pools mentioned above and farther upstream.

The condition noted above has not been observed since 1931. Since that time the stream has never been dry enough, to the writer's knowledge, to prevent water from flowing during the entire summer season.

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NOTE ON ATMOSPHERIC ARIDITY

The recent papers by Anderson,¹ Leighly,² and Curtis,³ to mention only a few, again call attention to the complexities involved in attempts to present an index of atmospheric aridity. Among the expressions of humidity—vapor pressure, relative humidity, dew point, saturation deficit, and wet bulb depression—each has its value; but would it not be much more useful for each investigator to publish the direct readings of the psychrometer, the temperatures of the wet and dry bulbs, from which the analytical reader could calculate whatever humidity expression suits his own needs?

¹ Anderson, D. B. 1936. Relative humidity and vapor pressure deficit. *Ecology* 17: 277-282.

² Leighly, John. 1937. A note on evaporation. *Ecology* 18: 180-198.

³ Curtis, O. F. 1936. Comparative effects of altering leaf temperatures and air humidities on vapor pressure gradients. *Plant Physiol.* 11: 595-603.

In recent preliminary work with the Livingston⁴ white, spherical, porous porcelain atmometer we have tried (a) to attain a more precise understanding of evaporation in relation to the climatic factors, and (b) to standardize the atmometer in terms of the environment.

As Leighley suggests, the measurement of vapor pressure gradient from atmometer to turbulent air would doubtless be an ideal expression of humidity in this case. However, we have not yet made such precise measurements. One hundred and seventy-five readings have been made mainly at two hour intervals of water loss from the atmometer, wind velocity with Robinson cup anemometer, sling psychrometer wet and dry bulb temperatures, and solar radiation with the Miller Radiometer.⁵ These have been made at Tucson, Arizona, and in the pine forest on the Santa Catalina Mountains. The data published by Johnston⁶ for observations in Maryland have also been used.

From these data it appears that evaporation from the atmometer is mainly a function of humidity and wind. The best correlation is obtained between evaporation and wet bulb depression, the relation being linear *for any given wind velocity*. The influence of wind velocity on evaporation is shown in the accompanying figure, each curve representing a *particular wet bulb depression*. A curve for each degree of wet bulb depression probably could be drawn, but we hesitate to do so now because of insufficient data and of the difficulty of accurately measuring wind velocity.

From zero wind movement to velocities of 3 or 4 miles per hour evaporation increases rapidly; further increases in wind velocity cause relatively small increases in atmometer evaporation. If the anemometer is placed even a short distance from the atmometer, the record of wind probably only approximates that which obtains at the atmometer. Since the relation of wind and evaporation is non-linear, an arithmetic mean of wind velocity is an inexact expression for long periods of time. Even for two-hour intervals some error is involved, and it is not surprising that arithmetic means of wind velocity for longer intervals have confused attempted correlations between wind and evaporation. Such a treatment of wind velocity, for long intervals, is sufficiently inexact to distort a correlation of evaporation and humidity for given wind movements. Wind velocity, furthermore, is such a complicated factor in climatic investigations that at present very little is known concerning wind conditions, vertically and horizontally, in plant communities.

The elevation above sea level and the coefficient of the individual atmometer are not to be neglected in the standardization of the atmometer. The rôle of solar radiation, although small, is appreciable. A sun shield over a white atmometer reduced evaporation an average of 0.45 cc. per hour on normal July days at Tucson. The sun shield cut out the direct solar radiation but not the sky radiation which was perhaps 25 per cent of the total. With the high evaporation rates at Tucson the sun shield reduced evaporation from 7 to 15 per cent, but with lower evaporation rates solar radiation may account for a much higher percentage of the water loss.

Preliminary efforts to correlate atmometers with open pans promise to be fruitful, although the relation is non-linear. The relation of one form of evaporating surface to another will probably be very complex in the last analysis, but daily totals smooth short time variations to sufficient extent for most ecological comparisons.

These studies suggest strongly that the Livingston atmometer can be standardized in terms of the environment, but that the difficulty of measuring climatic conditions out-of-

⁴ Livingston, B. E. 1915. Atmometry and the porous cup atmometer. *Plant World* 18: 21-30, 51-74, 95-111, 143-149.

⁵ Miller, L. F. 1937. Following solar activities with a new pyrliometer having a spherical absorber. *Bull. Am. Meteor. Soc.* 18: 213-220.

⁶ Johnston, E. S. 1919. Evaporation compared with vapor pressure deficit and wind velocity. *Mo. Weather Rev.* 47: 30-33.

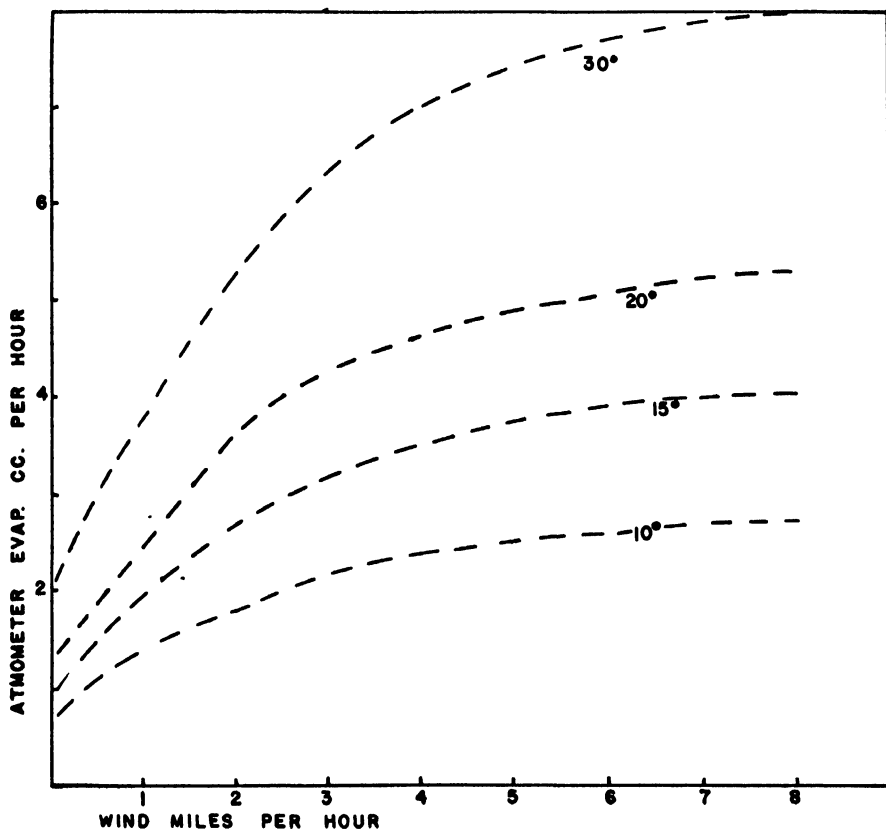


FIG. 1. Curves showing influence of wind velocity on evaporation at different humidities expressed in degrees Fahrenheit of wet bulb depression.

doors makes it necessary to standardize the instrument under controlled conditions. It is surprising that the many criticisms of the use of atmometers are based on so little quantitative evidence, and that so little has been done to determine quantitative differences in the relations of different evaporating surfaces to varying climatic conditions. Quantitative knowledge of the relation of various evaporating surfaces to climatic factors will contribute to a better understanding of the concept of relative transpiration.

In conclusion, we wish to emphasize that a presentation of both wet and dry bulb readings for humidity, and a detailed report of wind conditions are highly desirable in the publication of climatic data.

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THE INTERNATIONAL SOCIETY OF PHYTOSOCIOLOGY

This society is being organized with the following aims:

1. The development of phytosociology (and geobotany) by a closer collaboration between phytosociologists and ecologists.
2. The formulation of questions of phytosociological and geobotanical nomenclature destined to be presented to the International Botanical Congress and the ruling on questions of priority and validity of the systematic units of phytosociology or the terms used in geobotany.
3. The organization of excursions and scientific trips for the solution of certain scientific and economic botanical problems.
4. The creation of an international center of phytosociology in constant relation with the international and national committees. The International Station of Geobotany at Montpellier, France, is proposed as the center of the new society. This center would have the following functions:
 - I. To make available all general or specific bibliographical references on phytosociology, or geobotany, of the definite groups of vegetation which have been published.
 - II. To furnish information on the work in progress, on phytosociological mapping, on the groups of vegetation known but not yet published (tables of associations, charts of groupings, etc.), and on their geographical divisions.
 - III. To permit the consultation of the superior units of vegetation (alliances, orders, classes, etc.).
 - IV. To give addresses of reliable firms from which to procure apparatus of good quality for ecological measurements.
 - V. To publish an annual report giving notices and making known the decisions of the national or international committees.

Professor Szafer, Rector of the University of Cracovie, has accepted the presidency of the International Committee which is directing the affairs of the Society. National committees have been organized in France, Germany, Poland, Rumania, Jugoslavia, Netherlands, Belgium, East India, and Tropical Africa. The Acting Secretary from whom further information may be had is Dr. R. Tüxen, Landesmuseum, Hanover, Germany.

ECOLOGY

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ECOLOGY IN AGRICULTURE¹

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The major emphasis in ecological research, by ecologists, has been on native or wild plants and animals and not on cultivated plants and domesticated animals. Human ecology has also been largely untouched by ecologists. Scientists in other fields such as agronomy, horticulture, pathology, geography, sociology, and economics have not only been making increasing use of ecological concepts and procedures, but have been urging ecologists to broaden the scope of their investigations and teaching, so as to include the whole gamut of life in relation to the environment. The value of men who have been well trained in ecological technique and thinking has been long appreciated in forestry and range management, but now the call for help is coming from numerous additional fields. I am not advocating any diminution of interest and activity by ecologists in native plants and animals. We need to study these organisms under natural conditions much more than we have in the past in order to secure an adequate fund of basic information to use in planning improved relationships of people to the land. A few examples will be described to illustrate the need for ecologists to conduct research in crop plants.

At a recent conference of scientists and representatives of industry to consider ways and means to increase domestic production of flaxseed and to improve the quality of the oil, a prominent plant pathologist emphasized the need for a comprehensive study of the ecology of the flax plant. While much research has been done to improve varieties by breeding to control diseases, and to maintain yields by good agronomic practices, only a small start has been made in determining the relationships of the flax plant to soil and climatic conditions. Since one of the chief hazards in growing flax is its high degree of sensitiveness to changes in environmental conditions and since it is an important crop, not raised in sufficient quantity in the United States to supply the demand, it furnishes excellent material for the ecologist interested in plant-weather-soil relationships. It also furnishes a good op-

¹ Address delivered by the President of the Ecological Society of America at the annual dinner in Richmond, Virginia, December 28, 1938.

portunity to the ecologist who is interested in contributing to the solution of a serious agricultural and industrial problem by providing basic information about this plant. Other crop plants such as wheat, corn, cotton, sweet clover, and alfalfa provide numerous problems and abundant materials from a wide range of environments. The study in crop-weather relationships that is being sponsored by the Bureau of Agricultural Economics in cooperation with the state experiment stations in Kansas, North Dakota, Ohio, and Iowa, is an example of the ecological method of attack conducted cooperatively.

It is being increasingly recognized that reduction in damage caused by grasshopper infestations must be based on a foundation of ecological knowledge. The difficulties involved in the destruction of grasshoppers, such as the wide expanse of infested territory, the recurrence year after year of serious infestations, and the gigantic migrations such as occurred in the summer of 1938, can be solved only by a broad ecological attack. Poisoning alone is too expensive a method. The ecological foundation that must be erected for fully scientific control measures will be constructed from an assortment of building materials such as life history studies of various species of grasshoppers; interrelations of egg-laying, hatching, and other functions of grasshoppers to soils, vegetation types, and climatic factors; effects of various animals upon grasshoppers, including the requirements for sufficient shelter and nesting sites for birds and other predators of grasshoppers; effects of soil-conserving tillage methods and crop rotations upon egg-laying, egg-destruction, and hatching. Careful ecological study is needed to appraise the value to the farmer of burning weeds and brush in fence rows in relation to the need for shelter for birds and mammals that will prey on grasshoppers. What effect will artificial lakes and ponds, by providing favorable habitats for gulls, have upon control of grasshoppers? Will the reduction of wind erosion by grass buffer strips be offset by providing breeding sites in the strips for grasshoppers, cut-worms, and other insects? Additional interrelations of grasshopper control are found in overgrazing and regrassing of abandoned plowed fields. Serious grasshopper infestations may continue to occur in spite of all that man can do, but the ecologist, through research, can point the way toward reduction in the frequency and the area of the infestations.

An interesting ecological ramification started for me about 10 years ago when I visited the sagebrush-covered Laramie River Valley in northern Colorado. After consultation with ranchers, who needed more spring and fall range, an experiment was started in an attempt to secure more grass by burning the sagebrush. The thin stand of grass under the sagebrush was soon replaced by a phenomenal growth of grasses. In a short time an experiment station circular was issued describing how improvement could be secured in such areas. Satisfaction over the rapidly secured beneficial results of the experiment was soon faced with the objection that there was too much danger in burning sagebrush because such fires might spread to the forest. Further west another objection appeared. Burning of the sagebrush was following by growth of

annual weeds which was less desirable than the original stand. The sagebrush could be used to some extent, at least, as emergency forage and would catch the snow drifting with the wind, but the weeds were practically worthless. Additional complications were appearing meantime in Utah, Idaho, and California. Curly top, a virus disease, had been causing heavy losses in sugar beets, beans, and other irrigated crops. Control measures were not effective. It was baffling the plant pathologists until E. D. Ball found that the beet leafhopper was the vector transmitting the disease. Investigations by pathologists, entomologists, and ecologists soon revealed that the beet leafhopper builds up its numbers on annual weeds, especially green tansy mustard and Russian thistle, and that sagebrush and grasses are not important as host plants. The annual weeds occur as first invaders and in large numbers on abandoned plowed land, overgrazed and burned-over ranges. Under favorable conditions, this first stage in secondary succession is replaced in about five years by downy brome grass which is not infested. Burning of downy brome grass, which may accompany burning of sagebrush, delays further succession and favors reappearance of the annual weed stage. So, misuse of range and cultivated land is not only cumulative but far-reaching in its effects, and a practise considered beneficial in one area may have serious unsuspected consequences in another area. Burning of sagebrush and overgrazing may result finally in the distant, irrigated farmer losing his crops of sugar beets and beans.

This story shows the importance, in wise use of our land, of the climax or near-climax stage, with its perennial plants, not only in providing a more stable source of feed for livestock and protection for the soil, but also in providing protection for irrigated crops from insect infestations. Now when large portions of the western half of the United States are showing the serious, far-reaching consequences of grasshopper infestations, droughts, and various kinds of misuse, such as overgrazing, misplaced plowing, and improper irrigation, the call is becoming more insistent for the ecologist to help in unravelling the intricate interrelationships involved. Concepts and tools that are needed are methods of achieving harmonious relationships of organisms between themselves and to their environment, the concept of the natural tendency of community development toward stabilization with the environment, and the need for natural areas as checks, or standards, by which the values and effects of tillage, irrigation, drainage, grazing, lumbering, and other uses may be measured. I doubt that we need to dub as "agroecologist" the man working in these fields any more than we need the terms "hydroecologist," "arborecologist," "zoocologist," "phytoecologist" or even "bioecologist." Why not plain "ecologist"?

Social scientists who are "constantly wrestling with human problems" are seeking aid from ecologists, and the latter are responding. It was significant that four ecologists participated in the Conference on the Conservation and Development of Human Resources held in Washington, D. C., March 3-5,

1938. Other indications of this response are found in recent activities and writings of ecologists. Tansley in his review of Paul Sears' book, "Deserts on the March," presented some ecological relationships of the "urgent social problems which today confront every so-called civilized community" when he wrote: "Man's enormously increased technical knowledge and consequent power to interfere with natural processes have broken up the old stable equilibria of his community life in relation to its environment, and he is unable to construct new equilibria because of his want of foresight, and, it must be added, of his selfishness and greed. Science has given him the added powers and could tell him how they should be used, but will he listen? He is like a selfish and mischievous but vigorous child who has got hold of complicated and dangerous weapons or machinery. Morally he has never grown up, and his intellectual development is narrow and onesided. Better education in the use of reason and foresight, as well as in the social sense, seems the only hope, for it is true that these things can be taught. The future seems to depend on a race between the universal application of systematic efforts in such directions and the forces which are making for the wholesale destruction of our civilizations."

Dr. Tansley may be unduly pessimistic but he and Dr. Sears deserve much credit for clearly calling attention to the ecological aspects of many economic and social problems. It may be questioned, however, whether the ecological viewpoint is stressed sufficiently by Dr. Tansley. It is generally recognized that disturbances in the balances, or equilibria, of nature are always serious and require time for the processes of readjustment. The destruction of trees by fire, landslides, or parasites is followed by a series of successional stages that requires many years for the establishment of a new balance. Several generations of plants and animals follow one another in the adjustment processes. Each generation contributes something toward stabilization, such as organic matter to the soil, shade which favors growth of seedlings of the next stage, and increased retention of moisture. One generation or community of organisms usually makes conditions more favorable for the next generation of the same or different species. This process of natural succession, in which man plays no part, is generally recognized as being complicated and gradual. How much more intricate and difficult the processes of readjustment and stabilization become when man himself is involved as the chief dominant species in balance upsets! Attitudes of mind and long-established habits and customs are added to the numerous factors involved in non-human adjustment processes. In plants and animals, exclusive of man, we do not expect much change in one generation. Is not this same process of gradual adjustment also inherent in the relationship of *Homo sapiens* to his environment? I cannot agree with Tansley that man is unable to construct new equilibria because of lack of foresight, and because of his selfishness and greed. I have faith that man is inherently ecological, that he has enough in common with the rest of nature, in spite of his superior mind, so that he, too, cannot do otherwise

but take part in adjustment processes when stabilization has been disturbed. But, because of the numerous complicated interrelationships and modes of thinking that have become more or less fixed, it is probably too much to expect that this process of stabilization can be completed in one generation. I also have faith that man *is using* his brains to speed up the process of adjustment, and *because* of his superior mental powers the process will be more rapid than when lower organisms alone are concerned. As Tansley has indicated, it is one of our duties as ecologists to aid in securing a new balance by pointing out, not only how field operations as reforestation or regrassing can be hastened, but also to discover and to teach the ecological processes involved in human adjustment and stabilization.

May I be more specific? About 30 to 40 years ago, the fertile, gently rolling lands of northwestern North Dakota were homesteaded by hard-working farmers who saw opportunities to make a living by tilling the soil. Every encouragement by public and private agencies was given this invasion of the northern Gréat Plains grassland. The settlers were tillers of the soil, not ranchers or range men. Their mode of living, and their mental attitudes were adjusted to the plow, the harrow, the drill, the waving grain field, the threshing machine, a few livestock, and the farms comprising only 160 or fewer acres. Their mental and physical habits and customs were not adjusted to the necessities of the cowboy and sheep-herder; such as water holes, the wide range, corrals, good riding horses, and the round-up. At first wheat farming was restricted largely to the best land. During the World War much additional land was turned "wrong side up," due to the encouragement given to increased production of wheat. Many of these fields were located on slopes and on soils not suited to tillage. Since 1930, unfavorable conditions; droughts, wheat rust, insect infestations, and low prices have prevailed. Most of the farmers in this region, as fine a lot of industrious, enterprising people as can be found anywhere, have been reduced to poverty; the majority are now necessarily dependent upon governmental grants for their livelihood; a condition disliked by most of these farmers, but they are caught in the meshes of disturbed equilibria. They have been attempting to establish a relationship to the environment which was based upon, not only inadequate knowledge of this environment but, in some measure, at least, upon a relationship to a more eastern, moister environment. The farming methods and size of farm, suited to climatic and soil conditions in Iowa and Minnesota, have been demonstrated to be out of adjustment with the Great Plains environment. The years since 1930 have proved the impossibility of securing adjustment of the people to the environment chiefly by use of the plow and the wheat plant. Instead of gradual development of the community towards stabilization, the pioneers have often been making conditions less favorable, rather than more favorable, as should be the case, for the next generation.

Such disturbed equilibria have given occasion for many rash statements, such as the people are becoming "grant-minded" or "relief-minded" and the

entire area should be planted to grass and returned to wild life or to the Indians as quickly as possible. Such statements show insufficient recognition of the difficulties that even plant pioneers have in establishing themselves. Where conditions are highly variable, as in an active sand-dune area, along a shoreline or in an abandoned field, subject to overgrazing and drought, successive waves of migrants may appear before succession actually gets under way. The first plants to grow in such places may have the sand blown or washed away from under them or be killed by drought, leaving no successors. Ecologists may question whether even the first step in succession, namely, "invasion" has been accomplished under such conditions. Similarly, perhaps it may be questioned if the pioneering homesteaders have actually accomplished "invasion" throughout the region when there is considerable emigration, especially of the children, and abandonment of farms.

Conrad Taeuber and Carl C. Taylor in a paper entitled "The People of the Drought States," published in 1937, show in the following quotation, the similarity of sociological thinking with the ecological in regard to this difficulty of successful invasion:

Stability of residence itself is not necessarily a desirable goal, but the high degree of mobility which has been characteristic of the Great Plains Area indicates an unsatisfactory adjustment between man and his natural environment. Emigration as a technique for making adjustments is relatively inefficient for it provides little assurance of betterment to the individual and rarely strikes at the basis of the maladjustments involved. A high degree of mobility in a population impedes the proper functioning of those social institutions which are essential to a satisfactory farm life. Any successful program to adapt agriculture to the available natural resources would tend to reduce the volume of migration to and from the area. The success or failure of the efforts to control erosion and conserve available resources will be measured ultimately by the welfare of the people of the Great Plains Drought Area. Unless a satisfactory farm life can be developed on the basis of the resources of that region, no amount of modification of the physical environment will be worth while.

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Successful "invasion" has, of course, been accomplished in some localities and stabilization is beginning. Attainment by the people of equilibrium with the environment, or the development of a "climax" community, will be a slow process, but the essential steps are being taken. The people realize the need for more thorough knowledge of the environment and of the means for adjusting themselves by their processes and tools to the conditions of the region. This does not mean planting at once all tilled land to grass, but it means making use of all available scientific information in order to adapt their modes of living to the environment. It will probably mean restriction of wheat growing to the best land, more grass, more livestock, increased soil and water conservation, larger farming units, increased feed reserves, increasing aggregation of people into various kinds of groups, improvements in social institutions so they will facilitate further adjustment, and increasing emphasis on the eco-

logical point of view in planning so as to secure greater stability and higher standards of living. This will not be attained quickly, since numerous adjustments are needed in economic, psychological, and social processes and relations, in addition to the simpler physical operations. The ecologist, in this case which is typical of many others, realizing the time needed for stabilizing processes, will be patient. He can, also, be very helpful in applying the concepts of his science to promote stabilization in the Great Plains, in the southeastern states, in the cutover region of the Great Lakes states, and other regions where serious maladjustments between the people and their environment occur.

Permanent agriculture must be in adjustment with the environment. The United States is passing from its pioneering stage into more advanced stages. In too many regions, however, pioneering or invasion will be repeated, but it is hoped that it will be based upon a sounder knowledge of the environment. Stabilization of agriculture to the environment requires the services of scientists in many fields. The special contribution of ecology is to ferret out relationships with the environment so that man, using this knowledge in conjunction with that obtained from other fields, can strive intelligently to secure balance and stabilization, a goal essential for the attainment of the "abundant life" and the building of a culture far beyond our present dreams.

THE SONORAN BIOTIC PROVINCE

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The continent of North America is made up biogeographically of a number of biotic provinces (Dice, '31, p. 317), each characterized by the major occurrence of some important type of ecological community or by a group of related communities. The Sonoran is one of the most distinctive of these biotic provinces. It lies in the southwestern United States and northwestern Mexico and includes the Sonoran desert and some adjacent desert areas.

In the Sonoran province the temperatures of summer average exceptionally high, the scanty rainfall is soon evaporated, and conditions of extreme aridity result. Nevertheless, plants and animals occur all over the province and the desert as a whole is well populated. Neither the plants nor the animals of the desert are derived from a single line of ancestors. On the contrary, many different families of plants and of animals have become modified for desert life and in doing so have departed, sometimes slightly, sometimes very widely, from the characters of their relatives, some of which may be found still living in adjacent, less arid districts.

The biotic distinctness of the arid sections of the southwestern United States and northwestern Mexico seems first to have been recognized by Hinds ('43, p. 350-351), who, basing his description on the vegetation, named this district the "Chihuahua region." The Chihuahua region of Hinds includes parts of several other biotic provinces in addition to the Sonoran.

The term Sonoran was applied by various early zoologists to a faunal district in the Southwest, but the earliest adequate description of the "Sonoran Region" is apparently that of Cope ('73, p. 32-36), who centered the region in the State of Sonora, but included some areas which I place outside the Sonoran biotic province.

The Sonoran biotic province as here considered (Fig. 1) is bounded on the southwest mostly by the Gulf of California, but the province also includes the eastern shore of Baja California from about the 29th parallel northward (Nelson, '21, pl. 31; and Shreve, '26, p. 129-136). The western boundary of the province then continues northward through southeastern California to include the Imperial Valley, the Mohave Desert, and the adjacent desert valleys (Lower Sonoran life zone in part, of Grinnell ('35, pl. 3). The boundary then turns somewhat southeastward and crosses southern Nevada and the southwestern corner of Utah. From the Colorado River the boundary extends diagonally southeastwardly across Arizona to the southern end of the Rincon Mountains near Tucson (Nichol, '37, col. map). From this point

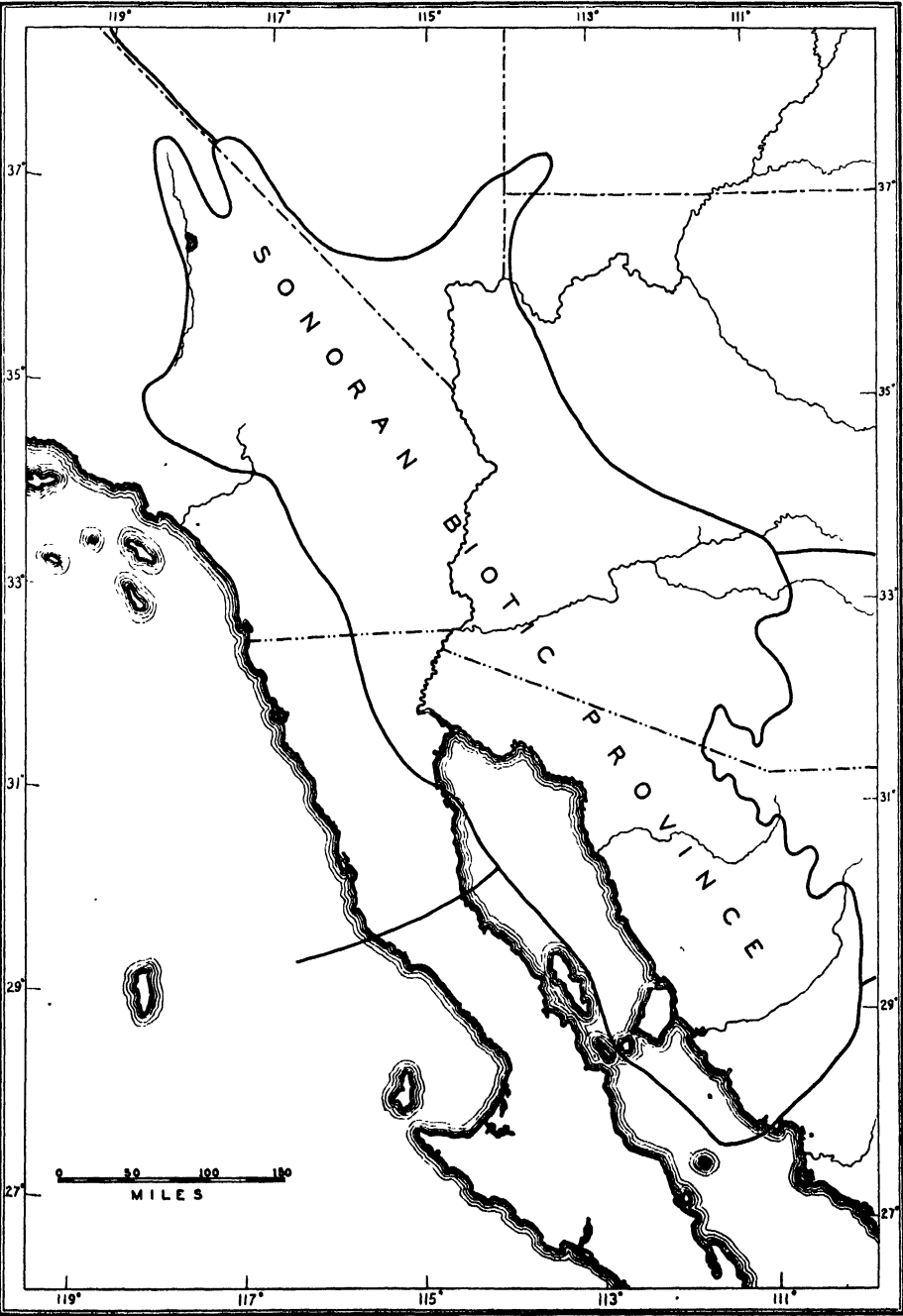


FIG. 1. Tentative map of the Sonoran biotic province.

the boundary circles westward around the northern end of the Baboquivari Mountains and crosses the Mexican border. It then extends southeastward across Sonora in a somewhat sinuous line to near Tecoripa (Burt, '38, Map 1). From Tecoripa the boundary runs southwestward to the Gulf of California, which it reaches near Guaymas. Some of the islands in the northern part of the Gulf of California are here included in the Sonoran province, but the biotic relationships of many of these islands are not well known. Later studies undoubtedly will require considerable modification in the here specified boundaries of the province.

Physiographic divisions included in the Sonoran biotic province are the Sonoran Desert section, the Salton Trough section, and a small portion of the Mexican Highland section of the Basin and Range province of Fenneman ('31, p. 367-369, pl. I). The Sonoran area is made up of alternating mountains and desert plains. The mountains have no regular orientation and their structure is irregular and mostly undetermined. Lavas and other types of igneous rocks are frequent. The drainage of most of this desert is good, though there are a few undrained basins. The Salton Trough and the Mohave Desert have entirely internal drainage.

The soils of the Sonoran plains are mostly fine in texture and gray or buff in color. There are, however, small local deposits of alkaline or volcanic soils. The alkaline soils are sometimes incrustated with whitish salts. The volcanic soils are of various colors, but are mostly dark in color tone. The desert mountains rise steeply from the desert plain and frequently expose bare rock cliffs. There are many slopes strewn with large and small rock fragments. The colors of the rocks vary in the various mountains from very pale granites to nearly black lavas.

The colors of these rocks and sands are ecologically important, for many of the desert animals tend to match the color of the soil on which they live. The soils of the desert plains are mostly pale in color and most of the desert animals are also pale in color, but those rock-inhabiting species which are restricted to the desert mountains vary in color from mountain to mountain, tending to be colored like the prevailing color of the rocks of the particular mountains on which they occur (Dice and Blossom, '37, p. 106-108).

The climate of the Sonoran province is characterized by high summer temperatures, slight precipitation, and low atmospheric humidities. At Yuma, Arizona, the average annual rainfall is only 2.7 inches (Henry, '06, p. 909). The rains are very irregular in distribution, but in general there is most rainfall during the winter months in the western part of the Sonoran area and most rainfall in the summer months in the eastern part of the area. The winter rains are usually, but not always, gentle and general in character, while those of the summer tend to be torrential local showers. The annual amounts of rain received vary greatly from year to year and periods of over a year may pass with no rainfall of sufficient amount to initiate plant growth. The temperature of the whole year averages very high in the Sonoran prov-

ince, the annual mean at Yuma being 72° F., and the January and July means are, respectively, 54° and 91°. Shade temperatures as high as 115° are not uncommon during the summer months. The winter temperatures average considerably above freezing, but frost may occur occasionally in winter anywhere in the Sonoran area. The atmospheric humidity is very low, especially in summer, due to the high air temperature and the low water content of the soil. At Yuma the mean annual relative humidity is only 41.6 per cent (Livingston and Shreve, '21, p. 344).

Neither the environmental conditions nor the fauna and flora are uniform throughout the Sonoran biotic province and a number of subdivisions, which should be called *biotic districts*, can be recognized. In Arizona the Tucson and Yuma biotic districts have been named (Dice and Blossom, '37, p. 66-74). I shall not attempt to describe other districts of the Sonoran province, but it is obvious that the Mohave Desert differs in numerous important respects from the desert of southwestern Arizona, and that the Arizona desert differs from the desert found further south in Sonora.

Numerous ecologic communities occur within the area covered by the Sonoran province and the sum of the areas covered by the several communities constitutes the province. These communities are related to one another in several successional sequences and in other manners. Not all the communities are of equal importance ecologically or biogeographically. Nor do all the ecological communities extend throughout the biotic province. Furthermore, some communities of the Sonoran province recur in more or less modified form in one or more of the adjacent biotic provinces.

The most characteristic plant of the desert plains in the Sonoran province is the creosote bush (*Larrea*). This often is associated, especially in overgrazed areas, with arborescent cacti (*Opuntia* spp.), locally called "choya." On the rocky slopes of the desert mountains the characteristic plants, are, near Tucson, the giant cactus or sahuaro, the ocotillo, and the palo verde. In Sonora a number of other conspicuous cacti occur. Along water courses the mesquite forms a typical community and some of the trees in this low forest have large trunk diameters. The mesquite also grows in a more open stand and in a more dwarfed condition in grassland at higher elevations.

The Sonoran biotic province as here defined agrees closely with the Western Desert Scrub, or *Larrea-Franseria* association of the *Larrea-Prosopis* formation, of Clements ('20, p. 170-177). This association constitutes the vegetational climax of the area. Clements, however, includes Baja California in the Western Desert Scrub, while I consider the southern part of Baja California to belong to a separate biotic province, the San Lucan. In the classification of Shelford, Jones, and Dice ('26, p. 72) the Western Small Tree and Succulent Desert biota corresponds in part with what I here call the Sonoran biotic province.

To the eastward of the Sonoran province the more abundant summer rains of the higher elevations support arid grasslands, which are often mixed

with open stands of mesquite. This area constitutes the Apachian biotic province (Burt, '38, p. 13-14), which Blossom and I ('37, p. 47-48) called the Chihuahuan biotic province. I now consider it better to restrict the name Chihuahuan to the desert which occurs in typical condition in the eastern part of the State of Chihuahua.

To the northeast and north of the Sonoran province lies a high plateau region on which the characteristic vegetation is a low open forest dominated by junipers, with which are often associated pinyon pine and various species of oaks. To this province I give the name Navahonian, from the Navajo Indian tribe. The presence of numerous kinds of cacti distinguishes the Sonoran province from the sagebrush area occupying the Great Basin, which I shall call the Artemisian province. In the Artemisian province the low-growing prickly pear is the only important cactus.

To the westward the Sonoran Desert changes, sometimes very abruptly, into the chaparral, oak forest, and valley grasslands characteristic of the Californian province, which has a dry summer climate. Baja California resembles the Sonoran province in its desert character, but it is itself an important center of differentiation (Grinnell, '28, p. 5-13) which is here recognized as a distinct biotic province, the San Lucan.

To the southeast, in the southern part of the State of Sonora, the Sonoran province meets the Sinaloan biotic province, which has a forest-free climate and which is characterized by thorn forest (Shreve, '34, p. 373-380). To explain the assignment of authority for the name Sinaloan to me by Burt ('38, p. 14) it is necessary to state that the present paper was prepared several years ago and that its publication has been delayed.

Many species of animals and of plants in the Sonoran province are closely restricted to particular ecological communities. Also some forms of life occur only in certain of the biotic districts and not over all the province. Furthermore, many races and local forms of plants and animals have differentiated on isolated desert mountains or on islands, or they for other reasons have only a limited distribution. It will be evident then that many of the peculiar Sonoran forms are not to be found throughout the province. To consider these forms as indicators of the province or even of any subdivision would be misleading. The province is characterized by the assemblage of forms there found together, and while the number of peculiar forms occurring in the Sonoran area indicates its distinctness from adjacent biotic provinces and its importance as a place of organic differentiation, yet the limit of distribution of no one of these "characteristic" forms "indicates" the boundaries of the province.

It is true that, if there is an important change in environmental conditions, a number of species and races may reach their limits of distribution at nearly the same line. Some species characteristic of the Sonoran province do not extend much if any beyond the limits I have mapped for the province. On the other hand, some other species, which are apparently equally as abundant

and equally as successful in the desert, extend far beyond the limits of the Sonoran area.

Some widely distributed species are able to range across several biotic provinces by being presumably adaptable in their ecologic toleration. Other species obtain extensive geographical ranges by occupying distant isolated patches of habitats similar to those which are characteristic of larger areas in the province where they are most abundant. A few species in each biotic province are characteristic of ecologic associations, such as the riparian association, which nowhere in the arid regions are very extensive, but which, nevertheless, may be widespread and important.

Sharp boundaries to biogeographical divisions are, in fact, rare, except where some barrier may completely limit organic distribution. Nearly all biotic boundaries are somewhat indefinite and ecologic provinces usually meet in a transition area which often is quite broad.

Many subspecies, species, and larger taxonomic groups of plants and animals are known to be closely restricted in distribution to the Sonoran province, but many groups of organisms have not yet been adequately studied in this and the adjacent areas, and I shall, in this paper, confine my remarks chiefly to the amphibians, reptiles and mammals. In preparing the following lists of mammals I have depended greatly upon the catalog of the mammals of the State of Sonora by Burt ('38) and the similar catalog of Californian mammals by Grinnell ('33). The lists of amphibians and reptiles were kindly prepared by Helen T. Gaige and L. C. Stuart. The mammal names used are those of Miller ('24) with later additions. The names of the amphibians and reptiles are from Stejneger and Barbour ('33).

The following species of mammals seem to be restricted rather closely within the limits of the Sonoran province as it has been above defined: *Citellus mohavensis*, Mohave ground-squirrel; *Perognathus formosus*, Creosote pocket-mouse; *Perognathus spinatus*, Spiny pocket-mouse; *Dipodomys mohavensis*, Mohave kangaroo-rat; *Dipodomys microps*, Kangaroo-rat; *Dipodomys deserti*, Sonoran kangaroo-rat; *Neotoma varia*, Woodrat. Also the species *Peromyscus stephani*, *P. collatus*, and *P. pembertoni* occur only on islands in the Gulf of California which are assigned to this province. These several species of *Peromyscus* are all members of the *eremicus* group which, as noted below, has numerous subspecies restricted to the Sonoran province. *Neotoma varia* is also restricted to an island in the Gulf of California. None of the species above listed are widely distributed in the province.

The following species of mammals are represented in the Sonoran biotic province by the subspecies stated, each of which is practically restricted to the province: *Vulpes macrotis*, subsp. *arsipus*, Kit fox; *Canis latrans*, subsp. *jamesi*, Coyote; *Felis concolor*, subsp. *browni*, Cougar; *Citellus tereticaudus*, subsp. *chlorus*, *eremonomus*, *tereticaudus*, Round-tailed ground-squirrel; *Ammospermophilus harrisi*, subsp. *harrisi*, *kinoensis*, *saxicola*, Harris antelope-squirrel; *Thomomys bottae*, subsp. *albatus*, *amargosae*, *cervinus*,

chrysonotus, *convergens*, *desertorum*, *mohavensis*, *perpallidus*, *phasma*, *puer-tae*, *vanrossemi*, Valley pocket-gopher; *Perognathus flavus*, subspp. *sonoriensis*, Silky pocket-mouse; *Perognathus longimembris*, subspp. *bangsi*, *bombycinus*, *kinoensis*, Pocket-mouse; *Perognathus amplus*, subspp. *rotundus*, *taylori*, Bahada pocket-mouse; *Perognathus baileyi*, subspp. *domensis*, *insularis*, Bailey pocket-mouse; *Perognathus penicillatus*, subspp. *angustirostris*, *minimus*, *seri*, *stephensi*, Wash pocket-mouse; *Perognathus intermedius*, subspp. *lithophilus*, *nigrimontis*, *phasma*, *pinacate*, Rock pocket-mouse; *Dipodomys merriami*, subspp. *merriami*, *mittelli*, *regillus*, *simiolus*, Merriam kangaroo-rat; *Castor canadensis*, subspp. *frondator*, Sonora beaver; *Onychomys torridus*, subspp. *clarus*, *pulcher*, Scorpion-mouse; *Peromyscus eremicus*, subspp. *eremicus*, *papagensis*, *pullus*, *tiburonensis*, Cactus-mouse; *Peromyscus crinitus*, subspp. *disparilis*, *stephensi*, *pallidissimus*, Canyon-mouse; *Neotoma albigula*, subspp. *mearnsi*, *seri*, *sheldoni*, *venusta*, White-throated woodrat; *Neotoma lepida*, subspp. *aureotunicata*, *auripila*, *bensoni*, *flava*, Cactus woodrat; *Sigmodon hispidus*, subspp. *eremicus*, Cotton-rat; *Ondatra zibethica*, subspp. *bernardi*, Muskrat; *Lepus alleni*, subspp. *alleni*, *tiburonensis*, Antelope jack-rabbit; *Lepus californicus*, subspp. *eremicus*, Black-tailed jack-rabbit; *Sylvilagus audubonii*, subspp. *arizonae*, Western cotton-tail; *Odocoileus hemionus*, subspp. *eremicus*, Mule deer.

There should be included in the above list several races of bighorn sheep, which have been described as *Ovis gaillardi*, *O. nelsoni*, and *O. sheldoni*, but which probably are geographic races of the wide-ranging species *Ovis canadensis*.

In addition to the species and subspecies which are listed above as being restricted to the Sonoran biotic province a number of other wide-ranging species of mammals are common in this province or at least in parts of it. Some of these species are represented in the province by more than one subspecies, none of which seem to be restricted to the province: *Macrotus californicus*, Leaf-nosed bat; *Myotis yumanensis*, Yuma bat; *Myotis californicus*, California bat; *Pipistrellus hesperus*, Canyon bat; *Corynorhinus rafinesque*, Lump-nosed bat; *Antrozous pallidus*, Pallid bat; *Tadarida mexicana*, Free-tailed bat; *Spilogale gracilis*, Spotted skunk; *Mephitis mephitis*, Striped skunk; *Mephitis macroura*, Hooded skunk; *Urocyon cinereoargenteus*, Gray fox; *Taxidea taxus*, Badger; *Canis latrans*, Coyote; *Lynx rufus*, Bobcat; *Citellus grammurus*, Rock-squirrel; *Ammospermophilus leucurus*, White-tailed antelope-squirrel.

Reptiles are very abundant in the Sonoran province, though amphibians are in general absent. The rattlesnakes (*Crotalus*), the bull-snake (*Pituophis*), and the whip-snake (*Masticophis*) are very numerous and characteristic. Lizards are especially numerous and the genus *Uma* is not found elsewhere.

The following amphibians and reptiles are restricted in general to the Sonoran biotic province:

AMPHIBIANS: *Bufo alvarius*, Colorado river toad.

LIZARDS: *Dipsosaurus dorsalis dorsalis*, Northern crested lizard; *Sauromalus obesus*, Chuckwalla; *Uma notata*, Ocellated sand lizard; *Callisaurus inusitatus*, Sonoran gridiron-tailed lizard; *Callisaurus ventralis gabbii*, Desert gridiron-tailed lizard; *Uta graciosa*, Long-tailed uta; *Heloderma suspectum*, Gila monster; *Phrynosoma m'callii*, Flat-tailed horned toad; *Phrynosoma solare*, Regal horned toad.

SNAKES: *Leptotyphlops humilis caluila*, Desert worm snake; *Lichanura roseofusca gracia*, Desert rosy boa; *Phyllorhynchus browni*, Brown leaf-nosed snake; *Lampropeltis getulus yumensis*, Desert milk snake; *Sonora occipitalis*, Tricolor ground snake; *Chilomeniscus cinctus*, Banded burrowing snake; *Crotalus cerastes*, Sidewinder.

TURTLES: *Gopherus agassizii*, Desert tortoise.

Besides the peculiar Sonoran amphibians and reptiles listed above a number of endemic forms occur on the islands in the Gulf of California.

In preparing lists of the forms of life characteristic of the Sonoran Province I have given little attention to subgenera, genera, or larger taxonomic groups. Taxonomic distinctness means mostly that intermediate forms have disappeared. Very distinct forms may, by reason of this distinctness, be indicated possibly to have been anciently separated from their allies. But forms with special adaptations to the desert environment may be connected through intergrading forms with allies which lack these adaptations. Degree of taxonomic distinctness, therefore, does not necessarily indicate the degree of ecological importance of the forms compared. Species, subspecies, or even local races may be ecologically as significant as genera or families, and I have in this discussion considered mostly the smaller taxonomic divisions.

Distinct varieties are particularly likely to develop in isolated habitats. Outstanding examples of local centers of differentiation in the Sonoran province are islands, water courses and springs, and isolated desert mountains and lava beds. The great number of isolated habitats in the Sonoran area has undoubtedly had much to do with the production of the considerable number of local races found in the province.

None of the subspecies or species of mammals, reptiles, or amphibians listed above as being restricted to the Sonoran biotic province can be considered to be relicts, that is, the remnants of forms which in some previous geological time had a wider distribution. On the contrary, many of the peculiar Sonoran forms give evidence of having originated on the areas they now occupy. This is particularly true of those forms restricted to small desert mountains or to islands in the Gulf of California. A number of these local races show, as stated above, a striking correlation between their pelage color and the color of the soil on which they live. Being apparently adapted to the particular environment in which they now occur these special forms are not likely to have originated at any other place.

That some of the subspecies characteristic of the Sonoran Province, and which probably originated there, will in time spread beyond the limits of the province is theoretically possible. But it has been shown (Dice and Blossom, '37, p. 109-115) that many of the peculiar Sonoran forms are restricted to very local habitats, which are probably also their places of origin. That these restricted forms will ever spread, as subspecies, much beyond their present geographical limits seems unlikely, for under present conditions natural selection should theoretically tend to eliminate any individuals which leave these particular environments.

That some forms originating in past ages in the Sonoran area may have spread beyond the boundaries of the province is nevertheless possible. Theoretically some of the forms originating in the desert and, therefore, presumably adapted to the desert environment, might be expected to spread into the more arid habitats of adjacent biotic provinces. It is possible, therefore, that many species which now have a wide distribution in Mexico and the western United States may have originated in the Sonoran province. A considerable number of species of mammals have distributional ranges whose geographical centers lie roughly in the Sonoran province.

The place of origin of any wide-spread species however, can rarely be determined with certainty and perhaps none of the species whose present ranges center in the Sonoran province actually originated there. Although Adams ('02, p. 122) and others have proposed criteria for determining the centers of origin of particular groups of animals these criteria are not universally accepted as valid by zoogeographers, the several criteria are not always easy of application to particular cases, nor are the indications from these criteria always consistent.

Our present palaeontological data also is generally inadequate to show the geographical locality where any particular genus or family has originated. The climatic changes over North America during the age of mammals, the Cenozoic, are believed to have been considerable. Correlated with these changes in the distribution of climates and of other environmental conditions great changes in the distribution of the various kinds of mammals and other animals as well as of plants must have occurred. All this was happening during the ages when the various living genera and species were being evolved.

Some genera of animals and of plants are now restricted to the Sonoran area and perhaps these groups originated there, but it is also possible that their origin was in some other locality. Other genera of animals or plants which do not now occur in the limits of the Sonoran province may have originated there, later spreading out. But for few if any of these genera would it be possible to prove any particular locality to be their center of origin.

A very confusing feature of all attempts to determine the place of origin of any group of organisms is that the parent stock itself must have had a place of origin. Every stage in phylogenic evolution must have had a still earlier ancestral stage. And the places of residence of the several ancestors,

and therefore the successive centers of origin for the stock, must at least occasionally have been in different geographical locations.

Little is known about the ecological factors which limit the geographical range of any of the desert animals. More is known about the factors which limit plant distribution, but it would probably be impossible to state for any desert species of plant or animal just what factors prevent its spread beyond its present limits of occurrence.

An arid climate has probably existed for a long period of geological time in and near the present site of the Sonoran province. We do not know how long the present type of wind circulation has been in existence on our planet, but it seems likely that it is not a recent development. With the present planetary air circulation the Sonoran Desert lies mostly within an area of persistent high pressure, with which is associated dry air and low precipitation. The position of the Sonoran area far south ensures a long hot season during summer, and the clear air allows the full strength of the sun to beat down on the parched soil.

The several ranges of California mountains tend to shut off winds from the Pacific and therefore extend the desert further north than it would otherwise occur, but it should be noted that nearly the whole of Baja California, lying directly beside the Pacific Ocean, is also desert. It is therefore obvious that the California mountains are not primarily responsible for the occurrence of desert in this area.

The extensive glaciation of the Pleistocene undoubtedly affected the climate of the Sonoran province to some extent, for at that time glaciers and snow fields were extensive in the California mountains. It is quite possible that during glacial time the climate of the Sonoran Desert may have been somewhat less severely arid than at present. However, the climatic influence of mountain glaciers does not extend to any considerable distance, and it seems very probable that a considerable body of desert or at least very arid climate continued to exist in the Sonoran area during the whole of glacial time.

How long before glacial time the Sonoran desert came into existence we do not know, but a long period of geological time would seem to be necessary for the production of the considerable number of peculiar, desert-adapted groups of animals and plants which occur in the Sonoran area.

According to Brooks ('26, p. 220-225) in Tertiary time the northern hemisphere in mid-latitudes was much drier than at present. If this be true, desert and arid conditions would have been much more widespread on North America than at present from the late Upper Eocene on through the Tertiary. The aridity of middle North America probably became ameliorated during the late Tertiary, as the glacial period approached. It is possible therefore, that the Sonoran biotic province is not the place of origin of all the peculiar Sonoran forms, but is an area of present concentration for a large number of species and races adapted to desert environments, some of which forms may have originated in other arid regions.

SUMMARY

The Sonoran biotic province is distinguished by its assemblage of species and races of plants and of animals. Many of the peculiar Sonoran races and species of amphibians, reptiles, and mammals have probably differentiated in the province, due evidently to the occurrence there of very distant types of environmental conditions combined with a considerable amount of local isolation. The Sonoran biotic province is also distinguished as an important physiographic province, as an important climatic province, and as a vegetation climax.

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A FOURTH EXPEDITION TO GLACIER BAY, ALASKA¹

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INTRODUCTION

In 1916 I made my first visit to Glacier Bay, initiating that year a long-time study of the reinvasion by plants of areas left vacant by disappearance of glacial ice. General observations were made, and permanent quadrats established in pioneer localities. The results from this and two later visits, in 1921 and 1929, have been published ('23, '31A, '31B, '31C).²

In 1935 Mr. William Osgood Field Jr. invited me to join him in an expedition to southern Alaska, the principal objectives being Glacier Bay and Prince William Sound. An opportunity was thus afforded for a fourth visit and a fourth charting of my quadrats. I wish to record my appreciation of Mr. Field's unfailing cooperation in the phases of the work in which I was particularly concerned, and also my thanks to Mr. Russell Dow and Mr. Robert L. Stix, our efficient assistants. Captain Thomas P. Smith of Juneau was, for the third time in charge of navigation. Three weeks were spent in Glacier Bay—the last of July and the first two of August.

It is quite natural that in such an investigation the glaciers themselves should receive much attention. Knowledge of their behavior and history is essential for understanding of the vegetational processes, and inclination would in any case have impelled me to give them as much study as possible. A purely glaciological publication was the result ('37), which embodies the contributions of others who have studied the region as well as my own.

For determination of plants collected during the 1935 expedition I am indebted to the following persons:

Pteridophytes and spermatophytes in general, Dr. Paul C. Standley; grasses, Mrs. Agnes Chase; mosses in general, Dr. R. S. Williams; sphagna,

¹ The publication of excess pages and illustrations in this article has been made possible by funds other than those of the Ecological Society of America.

² All citations refer to the author's earlier publications, as follows:

1923. The recent ecological history of Glacier Bay, Alaska. *Ecology* 4: 93-128; 223-246; 355-365.

1931A. A third expedition to Glacier Bay, Alaska. *Ecology* 12: 61-65.

1931B. The seed-plants and ferns of the Glacier Bay National Monument, Alaska. *Bull. Torrey Bot. Club* 57: 327-338.

1931C. The layering habit in Sitka spruce and the two western hemlocks. *Bot. Gaz.* 91: 441-451.

1937. The problem of Glacier Bay, Alaska: a study of glacier variations. *Geogr. Rev.* 27: 37-62.

Dr. A. LeRoy Andrews; hepatics, Miss Rosalie Weikert; cladoniae, Dr. Raymond H. Torrey.

The present account is not a complete summary of the investigation to date, but strictly a report of results obtained from the expedition of 1935. For the general background and conclusions the reader is referred to the publications cited above, especially 1923, 1931^A and 1937.

Description of the bay and its surroundings. Glacier Bay is a complex fiord, tributary to Icy Strait, 50 miles west of Juneau (fig. 1).³ Its greatest

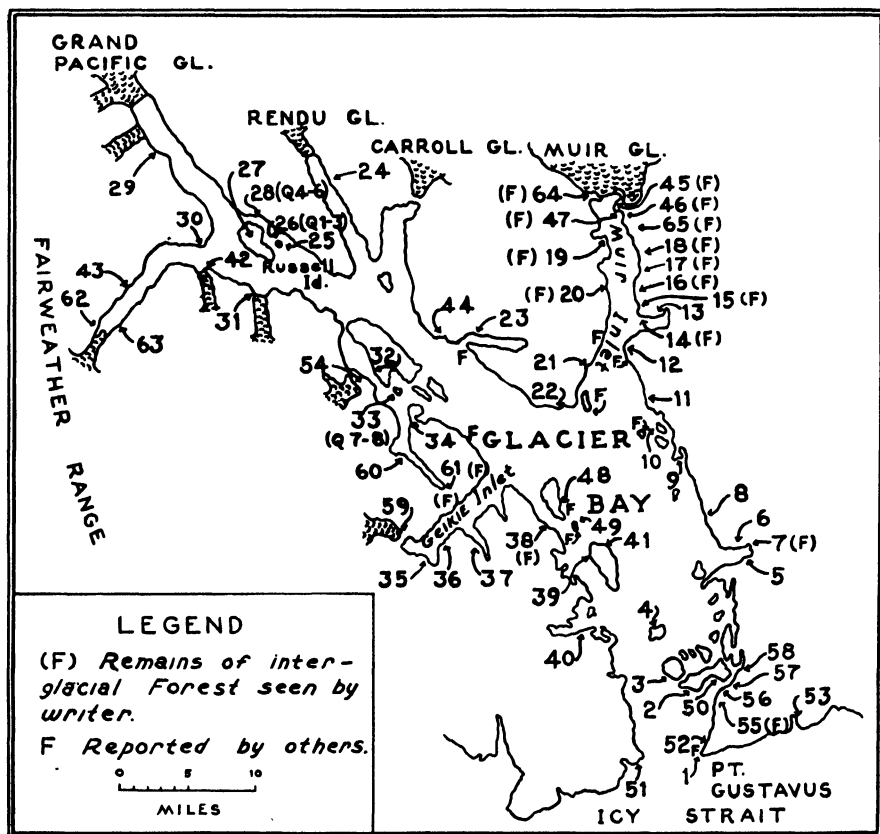


FIG. 1. Map of Glacier Bay, showing the principal geographic features, the location of all stations visited and of the permanent quadrats, and all known occurrences of ancient forest relics.

length is 60 miles. The lower portion is bounded by flat forelands and low mountains, and contains many islands of outwash and till. Next is an open expanse 15 miles long and 10 wide, surrounded by abrupt mountain slopes reaching altitudes of more than 5,000 feet. Northward, the bay is divided

³ A detailed map of the bay and its surroundings accompanies my most recent paper ('37).

into two main branches, Muir Inlet on the east, and the upper bay or north-west arm on the west. The latter is further subdivided, and its branches cut deeply into the heart of the Fairweather Range; the bounding walls of some of these attain altitudes of more than 8,000 feet. A multitude of glaciers of all sorts and sizes descend from the bordering mountains; in 1935 nine of these were discharging bergs to a greater or less degree.

Glacial history. Concerning the period since the Wisconsin maximum until comparatively recent time nothing can be stated except the self-evident fact of general glacial decline. In the twenty or thirty thousand years of this interval there were doubtless advances and retreats of which no evidence survives. There is clear proof, however, that some centuries ago the ice fields surrounding Glacier Bay were more contracted than they are today. The evidence consists in extensive gravel deposits resting on glaciated rock surfaces and overridden by the last advance and in the remains of forests preceding and contemporaneous with the deposition of the gravels. The minimum length of the period of contraction, for middle Muir Inlet, is indicated by the age of the oldest of the fossil trees whose rings were counted—383 years. Farther up toward the glacial sources the interval was shorter at both ends. For the lower bay it was longer, an estimate of a thousand years being surely not unreasonable.

The period of contraction was brought to an end when increased snow precipitation among the higher peaks initiated an advance of the glaciers. Converging upon the bay from all directions, these finally coalesced into a great trunk stream that discharged at the mouth of the bay directly into Icy Strait. From historical and ecological evidence this maximum is placed about 200 years ago.

The remaining history is, in the main, one of recession of phenomenal rapidity. The front moved back through the lower bay, became split into two when it reached Tlingit Point, and later suffered further subdivision. At the same time the ice was disappearing from the surrounding land, rapidly where the slopes were steep, more slowly where extensive lowlands were covered by a thick mantle of it. Recession is still the general order of the day, especially where ice still lies upon the lowlands.

Vegetational development. Correlated with the steady recession of the ice fronts during recent times is the contemporaneous advance of vegetation which has been the principal subject of my studies. It is taking place in three stages. The first is the pioneer community, in which the moss, *Racomitrium canescens*, the perennial herbs, *Epilobium latifolium* and *Equisetum variegatum*, the mat-plant, *Dryas drummondii* and the prostrate willows are the most important species. It is with the establishment and progress of this stage that the permanent quadrats are concerned. The second phase is the willow-alder thicket, composed of various species of bushy willows and *Alnus sinuata*. The final and climax stage has as its dominants the Sitka spruce, *Picea sitchensis*, and the two hemlocks, *Tsuga heterophylla* and *T. mertensiana*.

These three communities are displayed in consecutive order upon the shores of Glacier Bay. The pioneer group is found in scattered fashion in the upper reaches, the willow-alder thicket clothes the slopes of the middle bay and the young climax forest mantles the mountain sides and forelands surrounding the lower bay.

The feature that gives the region its unique value for successional investigation is the fact that glacier recession is measurable. Vancouver in the narrative of his explorations makes it possible for us to determine the approximate location of the ice front in 1794. John Muir and later visitors give very definite information concerning the status of the glaciers at more recent dates. It is thus possible to learn something of the *rate* of succession, concerning which our knowledge is as yet decidedly limited.

THE PRESENT VEGETATION CYCLE

1. *The foreland*

The extensive foreland east of the lower bay presents problems, both in glaciology and ecology, very different in nature from those provided by the upper bay with its precipitous slopes and many glaciers in close proximity. Typical terminal moraines with associated outwash, laid down at the most recent glacial maximum, give a close approximation to conditions existing at similar times in northeastern America during the Pleistocene. The edges of this area have been touched at various points during previous expeditions ('31*A*, pp. 87-88). In 1935 the interior was penetrated for short distances from three points on the shore of Bartlett Cove. Exploration is as yet quite inadequate for solution of the problems, but enough data have been obtained to warrant a brief account of the results to date.

Physiography. In describing the foreland physiographically, it is convenient to begin with the well-defined morainic belt associated with the maximum of two centuries ago (fig. 2). The southernmost point of it is at Point Gustavus, at the mouth of the bay. Here it is a few hundred feet wide, knolly, with marshy depressions. The material is silty, with no boulders visible in cut banks, but plenty in the water. From this point the moraine trends northeast, skirting the shore of the bay, to the mouth of Bartlett River. At Station 57A it is hardly more than a single ridge, at Station 58 it is a belt one-half mile wide. At these points it rises 100-120 feet above tide and 60-80 feet above the narrow terrace next the bay. The surface is conspicuously bouldery (fig. 3). Beyond Station 58 its course is unknown. On the south side of Beartrack Cove there is bouldery moraine, but this does not necessarily mark the extreme limit of the ice.

Outside the moraine (eastward), at least between Stations 56 and 58, there is a narrow strip of flat sandy outwash with abrupt pits. Beyond is a zone of rolling hills, parallel to the moraine, a mile or more wide. The material is medium to fine sand, with scattered pebbles up to four inches in diameter.

The broad, swelling ridges rise to a maximum of 150 feet above sea level, thus being higher than the summits of the moraine. The general altitude decreases gradually southeastward. This formation will be designated the "older outwash." Small deposits of dune sand lie here and there upon the surface, which in general is covered by a thin pebble concentrate.

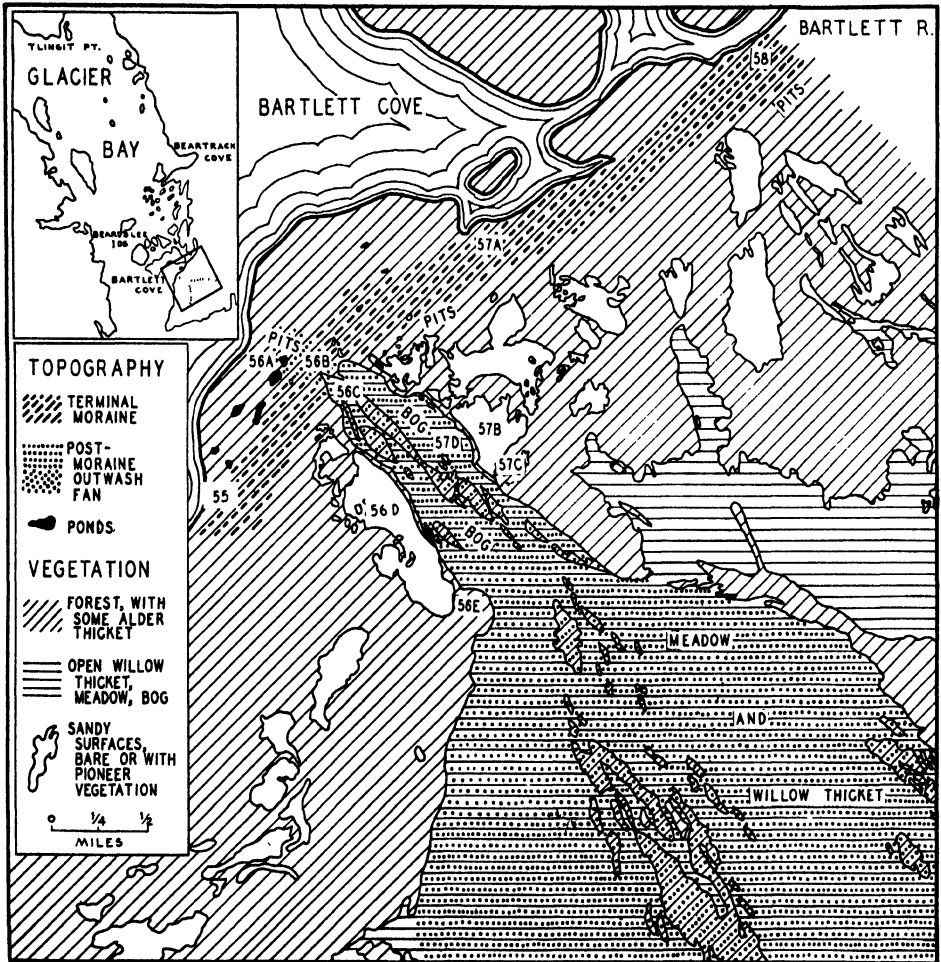


FIG. 2. Map of part of the foreland east of the lower bay, adjacent to Bartlett Cove. Based upon vertical photographs by Alaska Aerial Survey.

From Station 56A and B, a striking trough cuts southeastward for a mile and a half through moraine and older outwash. Its head, several hundred feet wide, is "in the air," so to speak, at the crest of a forty-foot bluff that descends to Bartlett Cove. The floor of the trough in general is about one-half mile wide, is flat and boggy, and stands about thirty feet above tide.

From its mouth issues a sheet of younger outwash, which spreads out fan-wise to the shore of Icy Strait. It is shallowly channelled and unpitted. The outer edge was described in the report of the preceding expedition ('31A, pp. 87-88).

Inside the moraine there are remnants of a level pitted plain at an elevation of 40 feet, bounded by a bluff descending to Bartlett Cove. The materials are like those of the older outwash outside the moraine. The Beardslee Islands, so far as observed, seem similar as to materials, but their surfaces are uneven and sprinkled with boulders.

The history recorded in these formations is clear enough in certain phases, but very uncertain as yet in others. All are associated with the recent maximum and beginning of recession. The older outwash definitely antedates the bouldery moraine. Its origin presents a difficult problem. Quite certainly, water has been the prime agent in its deposition. The deposits inside the moraine, especially those forming the Beardslee Islands, may be related in origin to the older exterior outwash. They were overridden by the ice which laid down the moraine, and portions were removed in irregular fashion, so that part of the surface now lies below sea level. The receding ice left behind it a thin scattering of ground moraine. The only subsequent modification has been the development of bluffs along the shores by waves and tidal currents.

The characteristic pitted outwash immediately in front of the moraine proves that the ice for a short time extended a little beyond its position.

As the ice finally receded from the moraine, drainage from a considerable portion of its front became concentrated at one point (Station 56A, B), cut through moraine and older outwash, forming the trough described above, and built the younger fan that extends to Icy Strait. It seems probable that for a time a proglacial lake stood where Bartlett Cove lies today. When its outlet at the head of the trough had cut down to 40 feet above tide, further recession of the ice front opened a way southward to salt water. The lake surface sank to sea level; the trough and fan, deprived of the water that had moulded them, have remained unchanged to the present day.

Vegetation. In describing the vegetation of the various phases of the foreland, the order adopted in the physiographic description will be followed. The moraine on the whole is rather densely forested (fig. 3). Spruce is most abundant, largest, and oldest. In the vicinity of Stations 57A and 58 they are 40-50 feet tall and up to 2.5 feet in diameter. Beneath the dominant stand are frequent small suppressed individuals, probably in part layered branches from the larger trees. Hemlocks (mainly *Tsuga heterophylla*, occasionally *T. mertensiana*) are fairly numerous as an understory, with a maximum diameter of 6 inches. Cottonwoods (*Populus trichocarpa*), as tall as the spruces, are also occasional. A few alders survive in openings. Fallen trees are fairly numerous, some recently overturned, others well rotted and thoroughly moss-covered. Some have numerous spruce seedlings growing on them. The general humus layer is about four inches thick. It lies upon

stones and gravel, and is topped by a dense carpet of mosses, the four characteristic forest species, *Hylocomium proliferum*, *Rhytidiadelphus triquetrus*, *R. loreus* and *R. squarrosus*, predominating. A similar mat covers the boulders almost completely. Aside from the mosses, undergrowth is sparse, consisting of a few shrubs, *Ribes laxiflorum* Pursh, *Fatsia horrida* (Sm.) B. and H., *Phyllodoce glanduliflora* (Hook.) Coville, *Sambucus pubens* Michx., and about a dozen herbs: *Dryopteris dilatata* (Hoffm.) Gray, *Polypodium vulgare* L. (on rocks), *Equisetum arvense* L., *E. variegatum* Schleich., *Lycopodium annotinum* L., *Streptopus amplexifolius* (L.) DC., *Epipactis decipiens* (Hook.) Ames, *Ophrys cordata* L., *Tiarella trifoliata* L., *Aruncus vulgaris*



FIG. 3. Bouldery terminal moraine of the last glacial maximum at Station 8, with sub-mature climax forest.

Raf., *Rubus stellatus* Sm., *Moneses uniflora* (L.) Gray, *Pyrola secunda* L., and *Boschniakia rossica* (C. and S.) Standley.

The forest here is approaching climax condition, yet both of the preceding successional stages are represented by relicts: the thicket by alder, the pioneers by *Equisetum arvense*, *E. variegatum* and *Phyllodoce glanduliflora*. The trees are of the first generation, shown by their branchiness to the base. The age of the community may be closely approximated from counts made on two 10-meter quadrats at Stations 57A and 58. In the first, the average age of 12 spruces was 101 years, the age of the oldest tree 121 years (borings here and elsewhere one foot from the ground). In the second, the average age of 18 spruces was 83 years, the age of the oldest 107 years. A few of the

younger individuals had probably originated from layered branches, so that the averages are too low.

The narrow strip of pitted outwash outside the moraine has features of special interest. The general surface is thinly covered with trees definitely younger than those on the moraine, and many thickets of alder occur. The pits, however, are crowded with trees of considerable size. One, not more than 50 feet across (fig. 4), contained a great triple-trunked spruce 4 feet in diameter at the base with individual trunks 18 inches thick, a 1-foot cottonwood, a 10-inch hemlock, several smaller spruces and hemlocks and a large clump of aged alders. Evidently the moist pit-bottoms provide optimum



FIG. 4. Pit in outwash exterior to terminal moraine at Station 8, containing luxuriant forest growth in marked contrast to sparser vegetation on the general surface.

conditions, while rapid drainage in the outwash makes the general surface less favorable even than the moraine.

The "older outwash" is characterized by striking lack of uniformity in rate of successional development. Every stage is present, from practically bare surfaces to forest equal in successional status to that upon the moraine (fig. 5). In the region explored—immediately north and south of the trough—the high rolling ridges support a thin population of pioneers, of a type quite different from that upon the freshly exposed gravels of the upper bay. Lichens are by far the most conspicuous plants. The following species were collected: *Cladonia coccifera* L., *C. squamosa* (Scop.) Hoffm., *C. uncialis* (L.) Web., *Stereocaulon* sp., and *Thamnolia vermicularis* (Swartz) Schaer. *Rha-*

comitrium canescens and other mosses are frequent, forming little mounds that stand out prominently, protecting the materials beneath from removal by wind. A few scattered herbs occur, the most frequent being the following: *Equisetum arvense* L., *E. variegatum* L., *Trisetum spicatum* (L.) Richter, *Carex pyrenaica* Wahl., *Habenaria hyperborea* (L.) R. Br., *Silene acaulis* L., *Anemone globosa* Nutt., *Dryas drummondii* Rich., *Astragalus alpinus* L., *Epilobium latifolium* L., and *Solidago multiradiata* Ait. Mounds of *Arctostaphylos uva-ursi* stand above the surface, both protecting it from wind erosion and causing local accumulation of sand. *Salix alaxensis* and *Populus trichocarpa* grow occasionally in the most exposed situations; the roots of the latter,



FIG. 5. "Older outwash" at Station 6. General surface with thin pebble concentrate; limited areas of dune sand. All successional stages: pioneers, thicket, climax forest.

bared by wind erosion, give rise to numerous sucker shoots. Lower, less exposed areas have a dense cover of lichens and mosses of the same species as listed above, and more abundant herbs. Here were seen *Fragaria chiloensis* and *Taraxacum officinale* (the latter probably an escape from cultivated lands of the pioneer human community on Icy Strait), seedlings of spruce and pine (*Pinus contorta*), and bushy willows (*Salix alaxensis* and *S. commutata*). *Salix barclayi* and *Shepherdia canadensis* are particularly associated with areas of dune sand, and *Arctostaphylos uva-ursi* is common also in such places. Scattered dead wood is evidence of long-continued but unsuccessful invasion by trees

Large expanses are covered by dense alder thicket, and considerable areas by forest like that upon the moraine. Two of the latter were studied. At Station 56E the forest is farther advanced than anywhere upon the moraine. Spruces occur up to two feet in diameter; four of the largest ranged in age from 123–133 years. Hemlocks are numerous, with diameter up to 20 inches, and occasional cottonwoods are present equalling the conifers in height. No significant environmental differences between forested and bare areas were discovered, either in substratum or topography. It may be that certain localities of small extent, slightly more favorable than the average, gave opportunity for the establishment of forest nuclei. From these centers the less favorable areas have been and are still being invaded by preliminary mass



FIG. 6. Trough cut through moraine and older outwash by glacial drainage stream in early stage of recession. Bog, meadow, and spruce groves on low ridges.

extension of alder thicket in certain places, and directly by spruce, pine and cottonwood in others.

The strip of flat pitted outwash between the moraine and Bartlett Cove bears forest like that upon the moraine, but slightly younger, judging from appearance and from a quadrat at Station 56A, where the average age of 16 spruces was 57 years and the age of the oldest tree 90 years. The forest on the Beardslee Islands is essentially the same.

The vegetation within the trough cutting through moraine and older outwash is in the main of bog type (fig. 6). It is best developed at the head of the trough (Station 56C). Here there is a quaking mat composed of sedges and grasses (*Carex limosa* L., *C. spectabilis* Dewey, *Eriophorum chamissonis* .

Mey., *Calamagrostis scabra* Presl.), abundant *Sphagnum squarrosum* Pers. and various bog herbs such as *Equisetum fluviatile* L., *Rumex occidentalis* Wats., *Epilobium palustre* L., *Hippuris vulgaris* L., *Nephrophyllidium cristagalli* Gilg, and *Galium trifidum* L. Open water appears in many places. Lower down in the trough the vegetation has formed a firmer mat, two phases of which are rather sharply distinguished. The wetter portions have a meadow-like appearance and support the following species: *Equisetum fluviatile* L., *E. variegatum* Schleich., *Agrostis hiemalis geminata* (Trin.) Hitchc., *Calamagrostis scabra* Presl., *Carex limosa* L., *C. rostrata* Stokes, *Eriophorum chamissonis* Mey., *Tofieldia intermedia* Rydb., *Habenaria viridiflora* Cham., *H. dilatata* (Pursh) Hook., *Spiranthes romanzoffiana* Cham., *Polygonum viviparum* L., *Rumex occidentalis* Wats., *Parnassia palustris* L., *Rubus stellatus* Sm., *Epilobium adenocaulon* Hausskn., *E. palustre* L., *Hippuris vulgaris* L., and *Menyanthes trifoliata* L.

The less wet places appear like a low thicket because of the abundant willows, especially *Salix commutata*. The following species occur here: *Bryum pseudotriquetrum* Schwaegr., *Calliergon cordifolium* (Hedw.) Kindb., *C. giganteum cyclophyllotum* (Holz.) Grout, *Camptothecium nitens* (Schreb.) Schimp., *Dicranum* sp., *Hylocomium* sp., *Marchantia polymorpha* L., *Philonotis fontana* (L.) Brid., *Equisetum variegatum* Schleich., *Carex aquatilis* Wahl., *C. brunnescens* Poir., *C. leptalea* Wahl., *C. viridula* Michx., *Juncus alpinus* Vill., *J. arcticus* Willd., *J. triglumis* L., *Tofieldia intermedia* Rydb., *Salix barclayi* Anders., *S. commutata* Bebb., *S. reticulata* L., *Drosera rotundifolia* L., *Empetrum nigrum* L., *Vaccinium oxycoccus* L., and *Pinguicula vulgaris* L. Long narrow strips of spruce forest occur on ridges that rise above the ground water table, and individual spruces are scattered over the meadow.

The fan of younger outwash which issues from the mouth of the trough supports a park-like growth of spruce groves and willow thicket, with wet meadow vegetation in the low places. This area was studied at its lower edge in 1929 ('31A), and the intervening territory is doubtless similar.

Two points of general importance emerge from this detailed study of the foreland and its vegetation. First, information is provided as to the length of time that has elapsed since the last glacial maximum, when Glacier Bay was filled completely with a great trunk glacier debouching upon Icy Strait. Up to the present, the evidence consists of the rather vague description by Vancouver of conditions as he saw them in 1794. He reports (see Cooper, '37, p. 47) that in that year "the shores of the continent form[ed] two large open bays, which were terminated by compact solid mountains of ice, rising perpendicularly from the water's edge and bounded to the north by a continuation of the united lofty frozen mountains that extend eastward from Mount Fairweather. In these bays also were great quantities of broken ice. . . ." Various writers ('23, p. 100) have inferred from this statement that, in 1794, Glacier Bay was occupied by glacier ice almost to its mouth. The reference to *two* bays has been a source of difficulty, and several explana-

tions have been attempted. Much more likely than any of these is the assumption that in 1794 the ice front had receded to the general vicinity of the Beardslee Islands, so that two tidal fronts were present—the main one west of the islands, the other, more than a mile in width, standing near the head of Bartlett Cove. The islands between, though low, would still be visible from the mouth of the bay. Assuming this condition, the ice, about 1800, should have receded perhaps a half-mile from the terminal moraine near the head of Bartlett Cove.

Study of the vegetation, though still leaving much to be desired in completeness, provides evidence which is entirely consistent with the historical records. Among 52 age counts made at three points on the terminal moraine, the greatest discovered was 121 years, at Station 57A. Allowing a few years for the first foot of growth, this tree began its life shortly after 1800. Establishment of the first spruces on the moraine at this date is entirely reasonable, since very early invasion of vacated areas is the natural thing where a source for seed is in such close proximity. It seems practically certain, therefore, on the basis of mutually consistent historical and vegetational evidence, that at the beginning of the nineteenth century recession was well under way. As to the time when recession began, there is still uncertainty. The period of maximum extension was presumably brief, judging from the small bulk of the terminal moraine. The paucity of ground moraine within the terminal argues for rapid recession. A mere guess of half a century before 1794 may be hazarded.

The second point is the rapidity with which a rich and varied vegetation may become established upon newly formed glacial deposits, provided sources for seed and spores are close at hand. All stages of the xerarch succession are present up to submature climax forest, and the hydrarch series is complete from open water through quaking bog and firm peat to willow thicket. The considerable formation of peat upon the floor of the trough, topographically the youngest feature, is noteworthy. In contrast, ponds and small lakes in the middle and upper bay region, some of which are more than half as old as the foreland, show as yet hardly a suggestion of the processes bringing about peat formation. The bottoms are of clean silt. The only true aquatic so far discovered are *Potamogeton filiformis* and *Ruppia maritima*. There is often a marginal zone occupying the shallow water and extending out over the gravels composed of *Equisetum arvense*, *E. variegatum*, *Eriophorum scheuchzeri*, *Carex vulgaris*, *Juncus haenkei*, and the mosses, *Philonotis fontana*, *Drepanocladus kneiffii* and *D. revolvens*. Of the carices and sphagna which are the really effective mat-formers there is as yet not a trace, while they are abundant on the foreland, close to sources for seed and spores. Evidently these plants are slow travelers.

2. Permanent quadrats

In 1916 I established nine permanent one-meter-square quadrats in three pioneer localities on the shores of Glacier Bay, in order to study the minute

events and changes which make up the stream of successional progress, and to discover as much as possible concerning the time factor in development. Unfortunately one of these was destroyed between 1921 and 1929 by erosion of the gravel terrace upon which it was located, but the other eight are safe from the danger of such disaster. The conclusions derived from the first period of five and the second of eight years have been presented in earlier

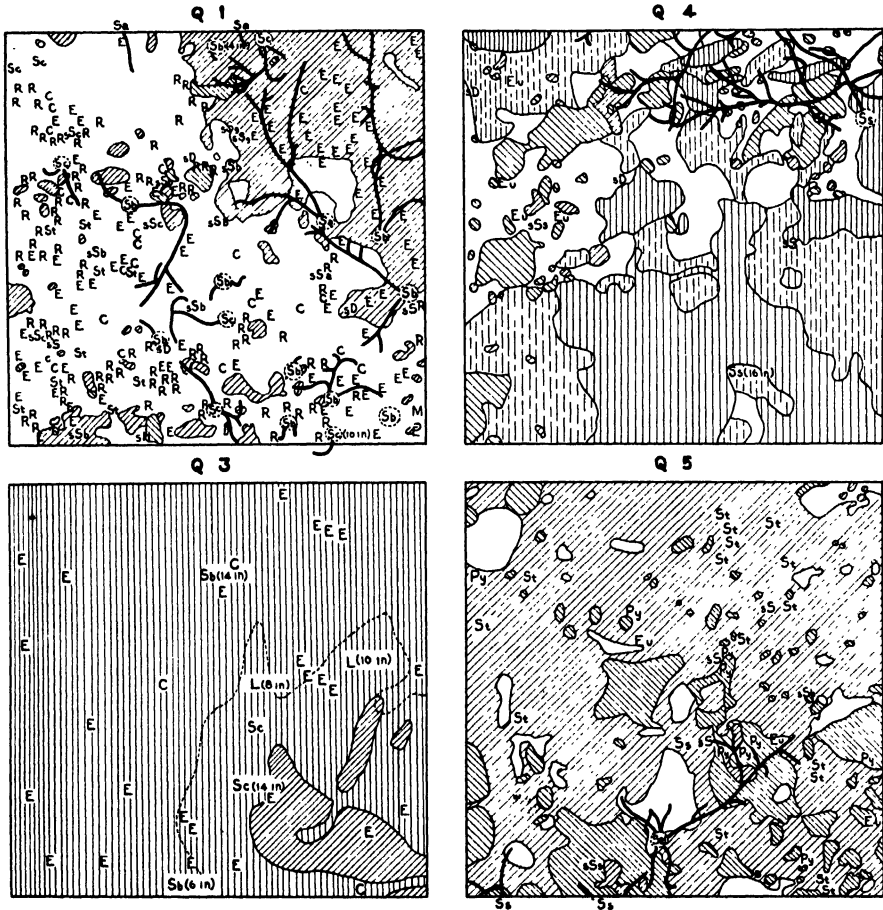


FIG. 7. Quadrats 1, 3, 4, 5 in 1935. Quadrat 2 is not shown, no change having occurred since 1921. For key to symbols see figure 8. Previous chartings of the quadrats of figures 7 and 8 are given in '31A, figures 3, 4, 5 and 6.

papers ('23, pp. 355-365; '31A, pp. 67-82). The locations of the quadrats are shown on the map (fig. 1).

In 1935 the localities were visited and the quadrats charted for the fourth time, and the progress up to that date is here recounted (figs. 7, 8).

The plant population falls naturally into three ecological classes: herbs (including *Arctous alpina*, a prostrate shrub of slight importance), shrubs

(all willows except an occasional *Shepherdia canadensis*), and mat-plants. In treating these groups it is necessary to make use of different criteria—number for the herbs, number and shoot-length for the shrubs, area for the mat-plants.

Herbs. Up to 1929 it was possible to trace the history of each individual from visit to visit, and thus to present figures showing mortality and “birth-

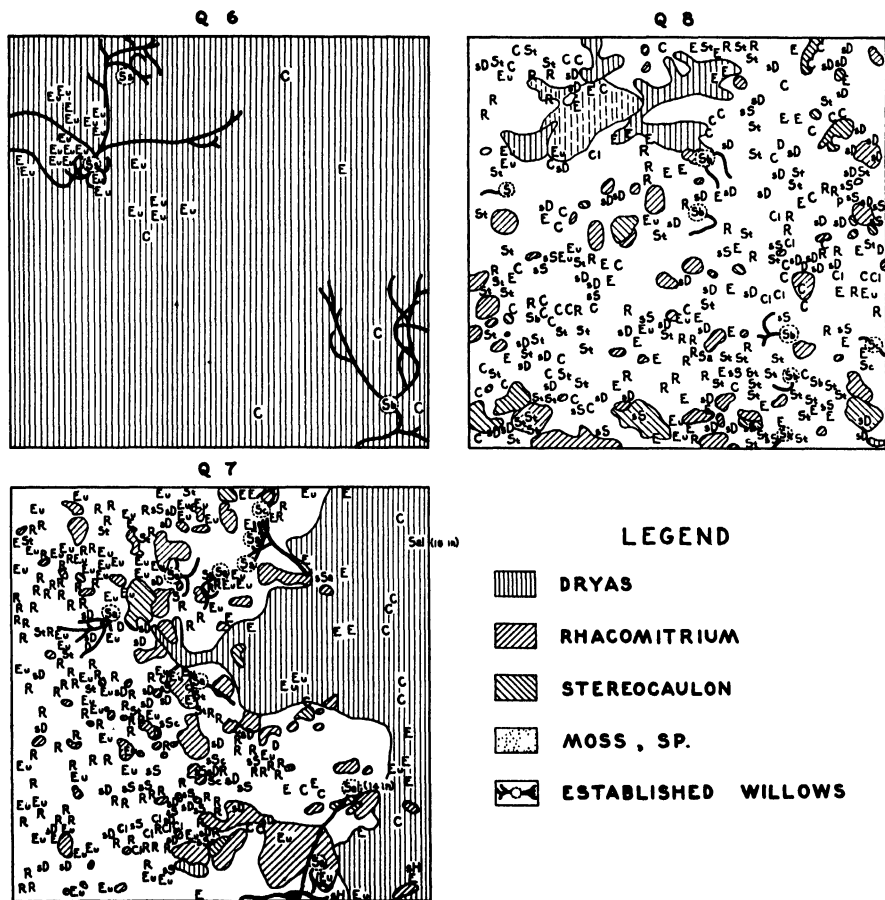


FIG. 8. Quadrats 6, 7, 8 in 1935. Key to symbols:

C	<i>Carex</i> sp.	Sa	<i>Salix arctica</i>
Cl	<i>Cladonia</i> sp.	Sal	<i>Salix alaxensis</i>
D	<i>Dryas drummondii</i>	Sb	<i>Salix barclayi</i>
E	<i>Equisetum variegatum</i>	Sc	<i>Salix commutata</i>
Eu	<i>Euphrasia mollis</i>	Sg	<i>Salix glauca</i>
H	<i>Habenaria hyperborea</i>	Sh	<i>Shepherdia canadensis</i>
M	<i>Marchantia polymorpha</i>	Ss	<i>Salix sitchensis</i>
Py	<i>Pyrola secunda</i>	Sst	<i>Salix stolonifera</i>
R	<i>Rhacomitrium canescens</i>	St	<i>Stereocaulon tomentosum</i>
S	<i>Salix</i> sp.	S,	prefix = seedling

rate." Due to increasing complexity of the plant cover this can no longer be done; it is necessary to be content with net totals. Table I presents statistics as to the herbs. During the period 1916-1921 the population sustained a net loss of 13.1 per cent, and from the latter date to 1929 a further loss of 3.2 per cent. The figures for 1935 show a striking gain of 64.8 per cent over 1929, and 38.6 per cent over 1916. This was due principally to *Carex* and *Euphrasia*.

Equisetum has continued its slow increase, and is still the most persistent of the herbs. *Epilobium* was abundant in 1916, but existing almost entirely as depauperate, non-flowering individuals. In 1921 it had been reduced to a very few, and in 1929 to a single individual. In 1935 it was entirely absent. *Carex* in 1935 showed a large increase over 1929 in two quadrats (Nos. 1 and 8). *Euphrasia*, first appearing in 1921, made a large increase between 1929 and 1935; one quadrat (No. 7) accounts for 63 of the total of 108 at the latter date. This species being an annual, such sudden bursts are to be expected.

The number of herbaceous species represented on the quadrats has remained small through the period of study—five in 1916, eight in 1921 and 1929, seven in 1935. During the last interval three new species had appeared, but four had disappeared. Of the three groups of pioneers the herbs, though conspicuous, are the least important as contributors toward successional progress, since their effects upon the habitat are least, and they have the least staying power in competition with others.

TABLE II. *Salix*; net totals and survivors 1916-1935

Established individuals								All individuals
	<i>S. alax- ensis</i>	<i>S. arc- tica</i>	<i>S. bar- clayi</i>	<i>S. com- mutata</i>	<i>S. sitch- ensis</i>	<i>Salix</i> spp.	Total	
1916	1	2	2		5	1	11	139
1921	7	9	10		16	7	49	140
1929	5	9	17		8	6	45	71
1935	3	5	17	8	7	1	41	110
Surviving 1916-1935	3	4	10	3	5		25	

Shrubs. In table II are set forth the net totals for the various species of willows occurring on the quadrats at each visit, and the numbers of individuals surviving from 1916 to 1935. The latter include some which have graduated from the seedling class during the period of study. Considering all individuals, the number remained practically stationary from 1916 to 1921, but by 1929 had been reduced by one half. A large increase appeared in 1935. Considering established individuals only (the presence of measurable prostrate or erect branches is taken as the criterion of establishment), a rapid increase from 1916 to 1921 was followed by a slow decline. Of the 41 present in 1935,

25 were survivors from 1916. Only 10 of the 41 were of the important species, *S. alaxensis* and *S. sitchensis*, which by reason of potential height growth are destined to form a part of the succeeding willow-alder thicket stage.

TABLE III. *Aggregate prostrate branch-length of Salix, all species*

	1916	1921	1929	1935
Aggregate branch-length	649.5 cm.	1568.6 cm.	2114.6 cm.	1839.1 cm.
Total increase or decrease		+919.1	+546.0	-275.5
Average per year		+183.8	+ 68.3	- 45.9

In 1929 the steady increase in aggregate length of prostrate branches was regarded as definite progress in successional advance. The charts for 1935 show death of many prostrate branches and the appearance of new ones, and table III demonstrates a considerable loss in aggregate length. There is compensation, however, in the first noteworthy development of upright shoots, which is the normal procedure when the plants become firmly established. Eight of these were present, ranging in height from 4 to 16 inches. There were also two individuals of *Shepherdia canadensis* of comparable height, new in 1935, on quadrat 3.

Mat-plants. Three common species are definitely mat-plants: *Dryas drummondii*, *Rhacomitrium canescens* (with some *R. lanuginosum*) and *Stereocaulon tomentosum*. From table IV it is evident that there has been constant rapid increase in all species. The actual rate is greater than indi-

TABLE IV. *Mat-plants on quadrats 1-8*

	Area	Increase	Average annual increase	Percent of total area covered
<i>Dryas</i>				
1916	26.65 sq. dm.			
1921	119.50	92.85 sq. dm.	18.57 sq. dm.	14.9%
1929	248.95	129.45	16.18	31.1
1935	355.00	106.05	17.67	44.4
<i>Rhacomitrium</i>				
1916	39.83			
1921	51.89	12.06	2.41	6.5
1929	71.30	19.41	2.43	8.9
1935	126.66	55.36	9.23	15.8
<i>Stereocaulon</i>				
1916	0.45			
1921	1.39	0.94	0.19	0.2
1929	22.35	20.96	2.62	2.8
1935	32.08	9.73	1.62	1.2
Moss sp.				
1935	1.79	1.79	0.30	
All mat-plants				
1916	66.93			8.4
1921	172.78	105.85	21.17	21.6
1929	342.60	169.82	21.23	42.8
1935	515.53	172.93	28.82	64.4

cated, due to the arbitrary limits set. The proportion of the total 800 sq. dm. covered has risen in nineteen years from 8.4 to 64.4 per cent. Three quadrats (Nos. 2, 3 and 6) are now completely occupied by mat-plants. *Dryas* is by far the most important of the three, the coverage having risen from 14.9 to 44.4 per cent. It completely fills quadrats 2 and 6. Four others are more or less occupied by it. The remaining two (Nos. 1 and 5) are as yet uninvaded except for two seedlings in quadrat 1. There has been since 1929 a very large increase in *Racomitrium*, and the increase in *Stercocaulon*, appearing suddenly in 1929, has continued. As noted in the last report, these two species seem doomed to elimination by the spread of *Dryas*.

The following changes in individual quadrats since 1929 are worth noting:

Quadrat 1. Little change in general. A new mat-forming moss, not a characteristic pioneer, first noted in 1929 but wrongly recorded on the published chart as *Dryas*, remains practically unchanged.

Quadrat 2 (chart not reproduced). Complete cover of *Dryas* since 1921.

Quadrat 3. Ground cover now complete. Area dominated by *Shepherdia* rooted outside quadrat, nearly bare in 1929, now occupied by *Racomitrium*.

Quadrat 4. *Dryas* dying out in places, and reinvading areas where dead in 1929, with some net increase.

Quadrat 5. Close approach to complete coverage by *Racomitrium*. Exposed position on top of ridge may possibly account for lack of invasion by *Dryas*. First appearance of *Pyrola secunda*.

Quadrat 6. Remarkably rapid invasion by *Dryas* since 1929, from seedlings within quadrat and mats outside it, resulting in complete coverage by this species.

Quadrat 7. Decided increase in *Dryas*, invading from right. Abundant sporelings of *Racomitrium* have appeared in left half.

Quadrat 8. Notable increase in individual plants of various species. Patch of *Dryas* in upper left, small in 1929, has spread considerably, dying at original center.

In the last report ('31*A*, p. 94) the successional progress up to 1929 was roughly divided into three phases. The period before 1916 (17–37 years) was characterized by dominance of perennial herbs, 1916–1921 by the firm establishment of individual willows, and 1921–1929 by great increase of mat-plants, especially *Dryas*. During the fourth period, 1929–1935, the mat-plants have maintained their dominant role. In addition, there has been the first noteworthy appearance of upright willow shoots, increase of which will finally lead to the next major successional stage.

3. Miscellaneous observations

Development at Station 26. This area, in which quadrats 1–3 are located, has received most careful study of any in the upper bay. It lies approximately upon the ice limit of 1879, so that in 1935 its subaerial history had covered 56 years. The vegetational development as recorded in the quadrats

is typical of the whole. The pair of photographs given in figure 8 of my last report ('31A, p. 81) indicates graphically the advance achieved in 13 years. *Dryas* is now so abundant as to give its tone to the whole landscape of the lower slopes.

The number of species has increased markedly in the nineteen-year period. A careful search in 1916 brought to light 21; in 1935 46 were noted, only four of the original list being unrecorded. The lists are of course incomplete, but it is safe to say that the flora has approximately doubled.

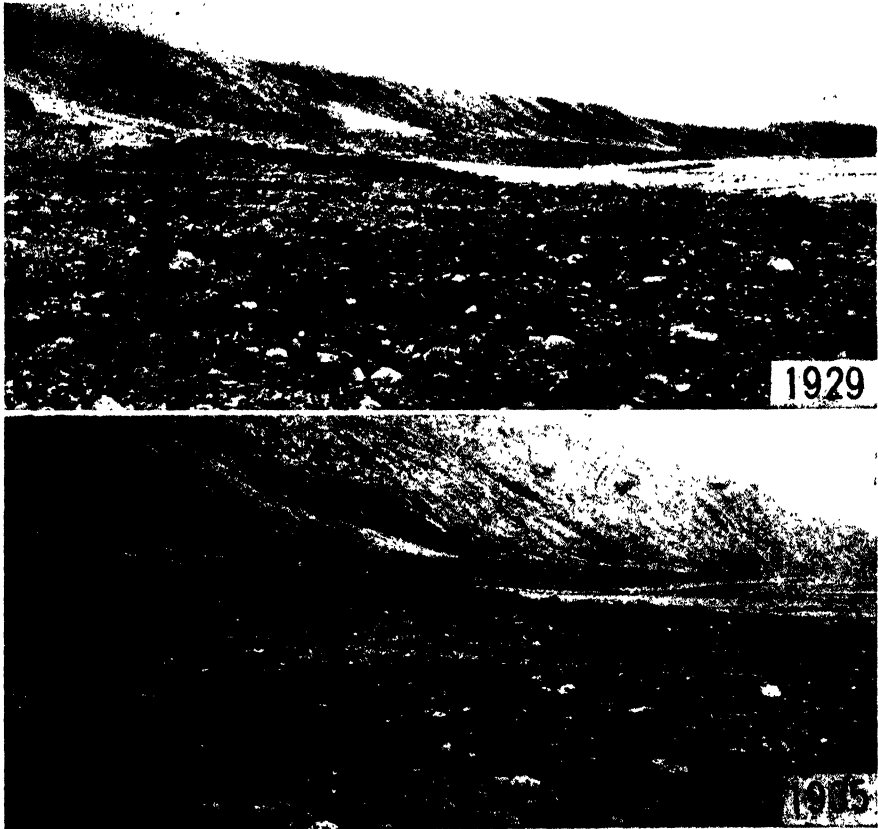


FIG. 9. Alder thicket at Station 26 in 1929 and 1935.

In 1929 I first noted the presence of a young alder thicket which previously had been so small as to be overlooked. This is described in detail in my last report ('31A, pp. 82-84). The oldest individuals, in the center of the thicket, were, in 1929, 12-14 years of age. They probably represent the closely grouped progeny of a single pioneer which had established itself several years earlier. A second zone was made up of individuals 6-7 years old, and scattered bushes outside of this ranged from seedlings to plants 3-4 years of age.

In 1935 the thicket had increased in area from one-half acre to three acres, and the central, oldest individuals from twelve feet to fifteen feet in height. Numerous scattered young bushes were found, as before, around the periphery, but absolutely none more than 250 feet distant from it. There were two small dense, detached colonies; the larger, on the upper side, was 35 feet in diameter and 150 feet from the edge of the main thicket. The pictures made in 1929 and 1935 (fig. 9) are exactly comparable, being taken from the same spot with the same lens. The thicket is shown also in figure 10.

Three tree species have already established themselves in the vicinity of Station 26: occasional matted spruces, and pines (*Pinus contorta*) and cottonwoods (*Populus trichocarpa*) 5–6 feet high. One-eighth mile inshore from the alder thicket, a spruce, 15 feet high in 1929, had grown to 25 feet in 1935



FIG. 10. Lone spruce at Station 26 in 1935. The alder thicket of figure 9 appears at left.

(fig. 10). In the latter year it was 6 inches in diameter, and a boring close to the ground revealed 26 rings. Growth during recent years had been rapid: the last ten rings account for nearly 60 per cent of the radius. There is no obvious reason why this individual tree should have so markedly outdistanced its companions. Its future history will be followed with interest.

Terrestrial animal life has begun to invade the region of Station 26. While I was studying the alder thicket a very lean wolf or coyote ran into it for hiding. Two miles northwest, near Station 28, I saw a large Alaska brown bear at a distance of a thousand feet, which, becoming aware of my presence, scrambled up the mountain side with incredible agility.

It is a long and difficult way to this spot from any region supporting a permanent population of these animals. The most likely route would seem to be from the upper tributaries of the Chilkat River at the head of Lynn

Canal, over the many miles of snowfields north of the Muir, Carroll and Rendu Glaciers. The food problem, too, in upper Glacier Bay is a serious one. There are no salmon, blueberries nor raspberries. *Shepherdia*, however, is common and fruits abundantly. There is proof that this species is utilized in the presence of bear droppings densely covered with *Shepherdia* seedlings of the current year. Since these berries were eaten during the preceding season, it is certain that one or more bears had arrived as early as 1934, and quite

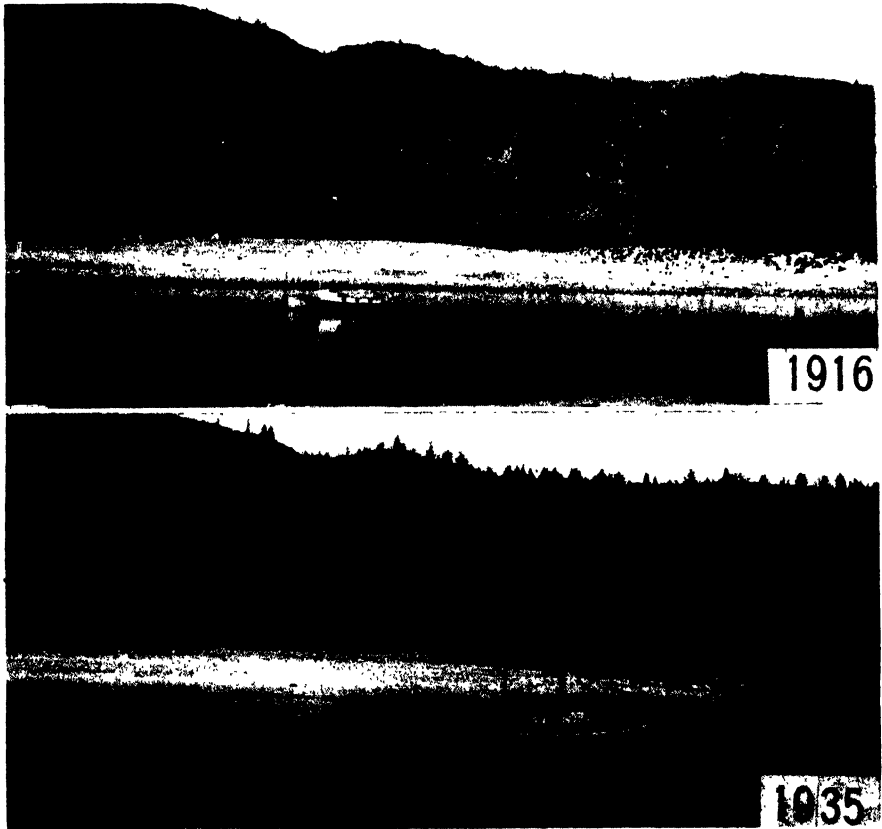


FIG. 11. Trees of climax forest superseding willow-alder thicket at Tlingit Point, Station 22. Development from 1916 to 1935.

probable that the one seen had over-wintered. As for the wolf's food supply, the problem is even more difficult.

Development at Station 22. On Tlingit Point, between the upper arm of Glacier Bay and Muir Inlet, there has been from the time of my first visit a conspicuous body of vegetation in process of transition from thicket to forest. It was studied and photographed in 1916 and again in 1929 and 1935. Figure 11 demonstrates the changes that had occurred in 19 years.

In 1916 the western portion was found to be clothed with willow thicket in which *Salix commutata* was most abundant. The substratum was a thick mass of detrital material, and the surface was relatively dry. In the eastern part there was a rather deep gully, and here the alders dominated. Scattered spruces up to 20 feet in height occurred throughout with occasional mountain hemlocks and cottonwoods. In 1929 a more thorough survey was made. Most of the spruces were found to have the clump habit, common in such situations and probably due to killing of the terminal bud during the first few years of growth and its replacement by several laterals. The diameters of the 15 trunks measured ranged from 9 to 22 inches. Layering was common; one tree had a circle of daughter trunks ten feet in radius, the individuals averaging 20 feet in height and 4 inches in diameter.⁴ Occasional seedlings were found beneath the alders, but almost none among the willows. The ground cover was luxuriant and composed of forest species rather than pioneers. A particularly interesting find for such a youthful community was *Cypripedium montanum*, the first record for Alaska.

Age counts of a number of the largest trees were made in 1916 and 1929. The average of ring counts from 15 spruces (adjusted to 1929) was 41.4; the highest was 53. Counts for one western hemlock and one mountain hemlock were 29 and 50 respectively. The average for 6 cottonwoods was 45.5 and for 7 willows 36.9. Based upon ring counts alone, the establishment of the spruces took place as follows: 1871–1880, 2; 1881–1890, 9; 1891–1900, 3; and 1901–1910, 1. Since a few years of early growth must be added to these figures, the maximum appearing in the eighties should be pushed back a little. It is a fair guess that the first spruces started here about 1870 and that establishment reached its maximum about ten years later. This locality is typical of the upper bay, where at points of known subaerial age spruces have not yet appeared, except sporadically, in periods ranging from 36 to 56 years after disappearance of the ice. An allowance of 40 years for the pioneer stage would place the disappearance of the ice at 1830–1840. The ice front must, then, have receded through the twenty miles of the lower bay from its supposed position in 1794 at the average rate of one-half to two-thirds mile per year. Further recession, from Tlingit Point to Russell Island (ice limit of 1879), works out to be practically the same. The vegetational evidence at Station 22, almost exactly halfway between the Beardslee Islands and Russell Island, thus indicates that recession between the two latter points has been uniform in rate.

The trees now present on Tlingit Point grew up with the willows and alders. All those sampled became established before 1900; for 35 years there has been no significant increase in number. There has been, however, notable increase in height and spread, well shown in figure 11; this with further growth of the daughter trunks from layered branches will steadily augment

⁴A detailed analysis of one of these layered branches has been included in a study of the layering habit in general ('31C, pp. 445–448).

the dominance of the trees and at the same time react disadvantageously upon the shrubs. It remains for future observation to discover whether the latter will be completely eliminated, with or without the coming in of new tree individuals.

INTERGLACIAL FORESTS

A feature of unique interest in the Glacier Bay region is the presence of relics of an earlier forest which flourished during the period of contracted ice fields preceding the late glacial maximum of about two centuries ago. Each visit has yielded new evidence as to its extent and character, which has been presented in two earlier publications ('23, pp. 93-127; '31*A*, pp. 88-93). A



FIG. 12. Interglacial forest at Station 65 in 1935.

brief general survey, including the observations of 1935, was included in a study of the glacial history of the region ('37, pp. 38-43). The present treatment will include descriptions of new localities discovered in 1935, with discussion of their bearing upon our knowledge of the forest as a whole.

In 1921 I found at Beartrack Cove, which lies at the northern edge of the foreland; a lonely hemlock stump below high tide line, evidently exposed by removal of the gravels that had overwhelmed it ('23, fig. 6, p. 109). This discovery led to the surmise that beneath the lowlands to the south more remnants lay buried. Verification came when in 1935 a group of stumps was found at mid-tide level on the south shore of Bartlett Cove. Samples from nine were examined microscopically: six were spruce and three hemlock. It appears that beneath the deposits that make the foreland and the Beardslee

Islands there lies a substratum which was clothed with climax forest during the period of glacier contraction. The present position of the stumps between tide limits shows that the surface upon which the forest grew must originally have stood at least slightly higher than now. It has not yet been possible to determine the nature of the substratum.

Muir Inlet has yielded by far the most numerous and interesting forest relics. In 1935 two new localities were studied, which added appreciably to our knowledge of the ancient forest.

Station 65 lies a mile and a half back from the east shore of Muir Inlet, in a deep wash made by torrential drainage from the Casement Glacier, a former tributary of the Muir, now rapidly shrinking (figs. 12, 13). The group of



FIG. 13. Near view of forest relics at Station 65.

decapitated trees was first seen by F. E. Wright in 1931. His photograph shows that only the part of the forest occurring on higher ground had come to light; water was flowing among the partially exposed trunks. By 1935 the stream had cut down 20–50 feet deeper. At one point it had reached bedrock and was plunging over a ledge in a tumultuous cascade. On the south rose imposing eroded cliffs of stratified gravels 200 feet high, at the base of which, in a few places, the old forest floor was visible. For the most part the substratum was still hidden beneath the terraced deposits.

The forest relics were found to be remarkably well preserved. The trunks, numbering at least two hundred, stood thickly together. In the vicinity of the cascade they were plainly rooted upon glaciated rock surfaces;

elsewhere the bases were concealed. Many still retained their bark, with mosses clinging to it. Small trees and the lower branches of large ones were many of them intact to the smallest twig. The humus layer which covered the rock surfaces was mostly thin and hard, almost skin-like, but in places there were sheets of perfectly preserved forest mosses. Great lengths of *Lycopodium annotinum* were found lying loosely upon the surface, washed out unharmed. Roots and branches contained in the peat were flattened by the tremendous pressure of the superjacent gravels.

The manner of burial seems to have been similar to that at Station 15 ('23, pp. 111–118): submergence of the forest floor followed by gentle deposition of silt. The living mosses and ground pine, thus embedded, were preserved intact beneath the load of gravels and of ice three thousand feet or more in depth. The underlying horizon of forest floor debris was compressed into a thin layer of compact peat. In view of the very complete study made at Station 15, which demonstrated the essentially identical character of the ancient and modern forests, no detailed analysis was made of the fossil plant remains. Fifty-seven standing trunks were sampled; 70 per cent were hemlock and 30 per cent spruce. This composition indicates that climax condition had been fully attained.

High up in the gravel bluff, very close to the top, an embedded log was seen. It had probably been carried down from the adjacent slopes, forested during the ice-free interval. Stumps belonging to this mountain-side forest were visible nearby in a rocky ravine several hundred feet above Station 65.

Station 64 is situated on the shore of a small inlet very close to the west end of the Muir ice cliff of 1935. Numerous stumps were seen, rooted either on a rocky slope or on two terrace levels. Of 25 trees sampled, 88 per cent were hemlock and 12 per cent spruce. Here too the climax had been attained.

In summary the expedition of 1935 made the following additions to our knowledge of the ancient forest: proof of the presence of climax forest on the foreland east of the lower bay; extension of the area dominated by climax forest northward in Muir Inlet as far as the ice had receded, and eastward to the mountain slopes that limit the bordering lowland.

At the beginning of my study I assumed that with continued recession of the Muir ice front and closer approach to its position during the period of minimum ice extension, less and less advanced stages of the succession would be laid bare; that hemlock-spruce climax would give way to spruce forest and this in turn to willow-alder thicket. The farthest accessible remnants in 1929 and 1935 gave no sign of such a progression.

Observations in Prince William Sound, made in 1935, suggest an alternative assumption. Here there are several straight-sided fiords, bounded by névé-laden cliffs and terminated by great trunk glaciers in which local climate or possibly abundant avalanching has inhibited the development of a continuous forest cover. Trees occur singly or in groups, and the individuals are of great age—from two to more than four centuries. They are main-

taining themselves close to the termini of the trunk glaciers, showing that these have not advanced perceptibly during the lifetimes of the trees. The prevailing vegetation cover is a combination of alpine turf mat and willow-alder thicket, both of which types may be as ancient as any forest.

It seems extremely probable that the Muir Glacier will continue its recession for some time at a fairly rapid rate, and that the fiord, as it opens up, will become narrower and steeper-sided. It may well be that the stabilized vegetation of the uppermost portion during the period of glacier contraction was like that of today in the fiords tributary to Prince William Sound. It is even more probable that such was the case in the inlets opening upon upper Glacier Bay, where, so far, no vestige of ancient forest has been found.

A THIRD YEAR OF MODIFIED BREEDING BEHAVIOR WITH RACCOONS¹

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INTRODUCTION

Previous studies with raccoons (*Procyon lotor*) showed that these animals can be induced to breed in December instead of in February and to drop litters approximately forty days earlier than normally. The early-born kits grew faster and larger than those born at normal time and were ready to fend for themselves in August. They were not induced to produce litters in their first winter by night-lighting, nor did they do so naturally. But two females, born at normal time and kept in a pen admitting more light by day than those used for experimental and control animals, dropped late litters sired by their littermate brothers. Many, if not all, experimentally lighted females went through second mating periods when returned to their male mates after pseudopregnancy, after killing their litters, or after weaning them. Four females produced litters from such second mating periods. Controls on normal light cycles mated only at one period beginning in early February (Bissonnette and Csech, '37, '38).

On a diet low in proteins for these animals (21.9 per cent), fewer litters were conceived and born than on the usual diet with proteins ranging between forty and fifty per cent. This was true particularly for animals on normal day-lengths and also to a less degree for those with experimentally lengthened daily periods of light. Desertion and eating of offspring seemed to be more frequent than usual, but it could not be attributed solely to the low-protein diet (Bissonnette and Csech, '38).

Since results of the experiments with low-protein diet were disappointing except for the second litters produced by some females after the diet was augmented to the usual proportion of proteins, the experiment has been repeated using the higher protein from the beginning and light bulbs of 25- and 40-watts.

MATERIAL AND METHODS

Controls consisted of twelve pairs (1 ♂ + 1 ♀) confined in pens similar to those used for experimental animals and described in previous papers, and an exhibition pen (no. 27) in which one male was confined with five females.

¹ Aided by grants from the National Research Council, Committee for Research in Problems of Sex 1937-38, and animals and their care from the Connecticut State Department of Fish and Game. *Modification of Mammalian Sexual Cycles: X.*

at first and again with two females later. This exhibition pen was similar to the one in which the two first year pregnancies described above occurred and it admitted more light to the animals by day than the experimental pens because it lacked the dark den in which the other controls and the experimental animals could hide from daylight. Experimental animals were ten pairs and three trios (1 ♂ + 2 ♀♀) in the type of pen used in former experiments. All animals were fed the same rations. Forty-watt bulbs were used with one pair (pen 2) and one trio (pen 9) and 25-watt bulbs with all the rest, in order to learn whether difference in light intensity lead to any significant difference in the time required to induce mating activity or in the size of litter. Breeding histories of many of the females were available for comparison of their performances under different conditions (Table VII).

Lights were turned on and off by a time switch for the following hours each day;—Oct. 20, 5–6 o'clock; Oct. 30, 5–7; Nov. 10, 5–8; Nov. 20, 5–9; Nov. 30, 5–10; Dec. 1, 4.30–9.30; Dec. 10, 4.30–10.30; Dec. 20, 4.30–11.30; Dec. 30, 4.30–12.30, each night for the following days until February 25, near term for experimental females. It was then discontinued for all animals and males and females were separated to give the females solitude while having litters and afterward.

OBSERVATIONS

Matings among experimental animals began later than in the two previous years, on or about December 28, and lasted until after mid-February. Con-

TABLE I. *Litters dropped by experimental females and their fates (1938)*

Order	Date	Serial no. of mother	Pen no.	Pair or trio	No. in litter	Reared (r) Abandoned (a) Eaten (e)
(1)	Mar. 7	17	8	Pair	5	5e
(2)	16	3	2	Pair	1	1a
(3)	19	9	5	Trio	3	3r
(4)	21	7 ^a	4	Pair	6	6r
(5)	22	2	1	Pair	3	3r
(6)	23	23	10	Trio	2	2r
(7)	25	21	10	Trio	5	2e + 3a
(8)	Apr. 3	51 ^a	3	Pair	2	2e (Apr. 10)
(9)	May 2	26	12	Pair	4	4r
Litters from second mating periods						
(10)	May 24 ^a	17	8	Pair	4	4e (May 31)
(11)	July 31	24 ^b	11	Pair	3	3r
(12)	Aug. 23	7	4	Pair	4	4r
Totals		10			42	25r + 4a + 13e

^a Litter born exactly 63 days after date of return to male. ♀ released June 1.

^b A good breeder but worthless as a mother.

Returned to male on April 18; no signs of mating again or of pregnancy; released into the wild on June 1.

^c This ♀ had no young from first matings a year ago but had 5 from second matings and reared all of them.

^d This ♀ had no young from first matings this year.

TABLE II. *Litters dropped by controls and their fates (1938)*

Order	Date	Serial no. of mother	Pen no.	Pair or trio	No. in litter	Reared (r) Abandoned (a) Eaten (e)
(1)	Apr. 4	45	23	Pair	4	4r
(2)	9	66 ^a	27 ^a	5 ♀ ♀ in exhibit pen with 1 ♂	3	3r
(3)	9	40	21	Pair	3	3r
(4)	10	47	31	Pair	3	3r
(5)	11	65 ^a	27 ^a	5 ♀ ♀ in pen, 1 ♂	2	2r
(6)	13	37	17	Pair	5	5r
(7)	13	64	34	Pair	4	4r
(8)	21	59	20	Pair	4	4a (as last year)
(9)	30	34	16	Pair	2	2r
(10)	30	— ^a	27 ^a	Trio	4	4r
(11)	May 6	39	18	Pair	3	3r
(12)	June 6	63 ^a	27 ^a	Trio	1	1 killed ⁷
Totals		12			38	33r + 4a + 1 killed

trols began to mate earlier than usual, on or about January 26, and continued until March 1 or even later.

No significant difference between the performances of animals lighted by 25- and 40-watt bulbs was noted so far as time of matings, of dropping kits, numbers of pregnancies, size of litter, or success in rearing litters. Tables I and II give the dates, numbers, sizes and fates of litters dropped by experimental females and controls, respectively, and the females liberated as useless for this type of propagation. Table III and IV give the same data

TABLE III. *Litters dropped by experimental females and their fates (1937)*

Order	Date	Serial no. of mother	No. in litter	Reared (r) Abandoned (a) Eaten (e)
(1)	Feb. 28	m	5	4r + 1a
(2)	Mar. 6		3	3a
(3)	6	o	4	4r
(4)	7		4	4r
(5)	9		5	5r
(6)	13		4	2a + 2e
(7)	19	a	3	3r
6 pens out of 13 gave litters; 7 ♀ ♀ out of 17 = 41%				
Total born = 28			Total reared = 20	

for litters from lighted and control females resulting from first mating periods in 1937 on the low-protein diet, for comparison with those this year on the normal-protein diet. Table V gives data on litters from second mating periods in 1937 which were conceived on the rectified diet of 40–50 per cent protein for comparison with such litters this year.

^a One ♂ was in an exhibition pen with 5 ♀ ♀ for a time; they were removed and a second lot of 2 ♀ ♀ added. He impregnated 4 of these ♀ ♀ in all.

⁷ ♀ released at once.

TABLE IV. *Litters dropped by controls and their fate (1937)*

Order	Date	Serial no. of mother	No. in litter	Reared (r) Abandoned (a) Eaten (e)
(1)	Apr. 17	—	4	4r
(2)	19	—	2	2a
(3)	May 15	—	3	3r
3 pens out of 13 gave litters; 3 ♀ ♀ out of 13 = 23 + %				
Total born = 9			Total reared = 7	

TABLE V. *Second litters from experimental females and their fates (1937)*

Order	Date	Serial no. of mother	No. in litter	Reared (r) Abandoned (a) Eaten (e)
(1)	July 27	7	5	5r
(2)	Aug. 12	a	1	1r
(3)	13	m	3	3r
(4)	18	o	1	1a
4 females out of 17 gave second litters = 23.5%				
Total born = 10			Total reared = 9	
Total kits born from experimental females = 38; total reared = 29.				

As shown in the tables, nine experimental females out of sixteen on adequate diet this year (1938) dropped litters from early light-induced matings and two of these repeated from second matings following their killing, eating, or weaning kits. Another female had a litter from the late mating period after failing to conceive or being only pseudo-pregnant at the first matings. These give totals of forty-two kits born, twenty-five reared. Twelve control females out of nineteen produced thirty-eight kits born, thirty-three reared.

TABLE VI. *Records of kits born and reared per ♀ used and per ♀ reproducing*

Year	Diet in protein	Kits per ♀ Born	used Reared	Kits per ♀ Born	reproducing Reared
Experimentals 1937	Low	$\frac{38}{17} = 2.235$	$\frac{29}{17} = 1.70$	$\frac{38}{8} = 4.75$	$\frac{29}{8} = 3.625$
1938	Adequate	$\frac{42}{16} = 2.625$	$\frac{25}{16} = 1.563$	$\frac{42}{10} = 4.2$	$\frac{25}{10} = 2.5$
Controls 1937	Low	$\frac{9}{13} = 0.692$	$\frac{7}{13} = 0.538$	$\frac{9}{3} = 3.00$	$\frac{7}{3} = 2.33^a$
1938	Adequate	$\frac{42}{19} = 2.21$	$\frac{25}{19} = 1.316$	$\frac{42}{12} = 3.5$	$\frac{25}{12} = 2.083$

^a These females were receiving adequate protein diet during most of their gestation periods and all of their suckling periods. So the effect of low protein diet is not operating during those periods.

TABLE VII. *Complete breeding records of experimental and control females having litters in 1938*

Serial no. of mother.	1935	1936	1937	1938	Disposal
Experimentals:					
17			4r	5e + 4e	Freed June 1
3	4r	4r	0	1a + 0	
9	1r	1r	3r + 3r	3r + 0	
7		6r	0 + 5r	6r + 4r	
2	3r	3r + 0	3a + 0	3r + 0	
23			3r	2r + 0	Freed June 3 Freed
21		0	(2e + 2a) + 0	(2e + 3a) + 0	
51				2a + 0	
26			0	4r + 0	
24	4r	4r	4r + 1r	0 + 3r	
Controls:					
45	Born 1936 from lighted parents		0 (at 1 yr)	4r	
66	Born 1936, normal parents			4r	
40		0	0	3r	
47		1r	2r	3r	
65				2r	
37			4r	5r	
64				4r	
59	Born 1936, normal parents		2a (exhibit pen)	4a	Freed
34			0	2r	
—				4r	
39		1r	3r	4r	
63				1a	Freed

On the low-protein diet of 1937, seven experimental females out of seventeen produced first litters and four dropped litters from second mating periods. Of these, three were repeats and one was from a female failing to become pregnant at the first mating period. These give totals of thirty-eight kits born, twenty-nine reared. Only three control females out of thirteen dropped nine kits and reared seven.

Females 17 and 7 gave interesting breeding and rearing performances. No. 17 produced the earliest litter dropped this year, on March 7, placing her date of impregnation on January 3, if her gestation periods were of equal duration. She ate the five kits within a week of their birth. Returned to the male on March 22, she produced four more kits on May 24, exactly sixty-three days later. This indicates strongly that her gestation period was sixty-three days or less, not more. This is the period generally believed to be correct for raccoons, but with little previous positive evidence. The second litter preceded that of the latest of the controls, one kit on June 6. Again she ate all her kits within a week of their birth, on or before May 31. She had produced and reared a litter of four kits on normal days in 1937.

No. 7 dropped litters of six and four kits on March 21 and August 23 of the same year and reared all. In 1937, although she produced no kits from early light-induced matings on low-protein diet, she dropped a litter of

five kits from second matings on adequate diet and reared them all. In two years on experimental lighting she produced fifteen kits and reared all. In 1936, on normal light and adequate proteins, she dropped and raised six kits to bring her total for three years (one without lighting) to twenty-one kits without abandoning any.

DISCUSSION

The records of females 17 and 7 show that not all good breeders are good mothers. Failure of many females to breed at all under either normal or experimental conditions makes it necessary to select for good qualities as mothers in addition to breeding capacity. No. 17 was successful under normal conditions in 1937 both as breeder and mother; but under lighting conditions she succeeded only as a breeder, possibly because of too nervous temperament. She was also either more susceptible sexually to increasing length of day, or mated with a male of high susceptibility, or both. Her first litter was the earliest of the group. No interference with her kits nor improper diet can be blamed for her behavior. Her litter conceived on low proteins last year was reared and both litters conceived and born on adequate diet this year were killed and eaten, though she was not disturbed in the latter case at all. This indicates that some female raccoons may be excellent breeders but, at the same time, temperamentally unfit to rear young on night-lighting schedules. They are therefore useless for this purpose and cause needless expense (Table I).

No. 7, on the contrary, presented the happy combination of excellent breeding capacity on both night-lighting and normal daylight schedules. She was either less susceptible to sexual stimulation by night lighting or mated with a less sensitive male; she came into breeding effectiveness later. She also possessed an excellent temperament for rearing her young and high milking capacity. She belongs to the type of female from which to breed by night-lighting in autumn to produce large numbers of raccoons at small cost, and the type to liberate for high production under natural conditions (Tables I, III, V, VII).

Other categories of raccoons and numerous intergrades of breeding and rearing capacities are illustrated in the tables, from complete failure to breed to capacities like those of the two females described above. Ineffective females, from whatever cause, should be liberated as soon as their failures are determined, to keep down expense. Animals are sometimes effective under natural conditions but not under experimental lighting and *vice versa*. Only testing under both conditions can settle this matter. The fact that the males must also be tested by trying females with more than one male before discarding them is shown by these results. The male, in the exhibition pen, used as control, impregnated four females, two of the first five confined with him and both of the later pair. This indicates that a good male can cover at least four females effectively.

SUMMARY

(1) Twelve pairs of raccoons in experimental pens and one male confined in an exhibition pen, first with five females, then with two others, were used as controls on normal day-length.

(2) Ten pairs and three trios (1 ♂ + 2 ♀♀) were exposed to night-lighting increased one hour each ten days, beginning October 20, to eight hours per night from December 30 to February 25. One pair and one trio were lighted by 40-watt bulbs, the rest by 25-watt ones.

(3) Rations for all animals contained 40–50 per cent of proteins.

(4) No significant differences in effect between 40- and 25-watt bulbs were noted.

(5) Experimental animals began to mate later than in two previous studies with lighting begun earlier and coming more quickly to the maximum 8-hour daily lighting period. This indicates that time of beginning or rate of increase of experimental lighting, or both, affected results.

(6) Controls began to mate earlier than in previous years, probably because this less rigorous winter failed to induce "pseudo-hibernation" with its consequent reduction of light affecting animals "holing up" in dark dens.

(7) One control male impregnated four females confined with him at different times.

(8) Second litters in the same season were produced by two experimental females and one produced a late litter after failing to be impregnated at early light induced matings.

(9) Comparison with results on a previous low-protein diet indicate that experimentally lighted animals are much less adversely affected by the lack of proteins than animals on normal light cycles so far as number of pregnancies is concerned.

(10) Breeding and rearing performances of some females show that not all good breeders are also good mothers. Breeding stock should be selected from those best in both respects or from animals most nearly approaching them, using males of proven effectiveness, and their progeny. Continuous rigorous selection for these qualities should be carried out under experimental conditions.

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THE ECOLOGICAL PROBLEM OF MYCOTROPHY

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The idea of mutually beneficial symbiosis, offensive to so many biologists, seems superfluous as far as the orchid mycorrhiza is concerned. Most of the orchid fungi thus far tested have been found to thrive when growing alone on leaf litter, wood, etc. (Holländer, see Burgeff, '36). Several species have even formed fruiting bodies in pure culture on such substrates (*Armillaria mellea*, *Marasmius coniatu*s var., *Xerotus javanicus*). Such saprophytic fungi do not need the orchids, but the orchids need them either permanently (chlorophyll-free species) or at least for getting a start in life. The relation appears to be a parasitism¹ of the orchid on the fungus (Burgeff, p. 280).

Different in principle is, according to accumulated evidence, the symbiotic relation between conifers and their mycorrhizal fungi. Everyday experience in forestry shows that trees, in their food habits, are not parasitic on their mycorrhizal fungi as some orchids appear to be. These fungi, on the other hand, behave much like parasites on the trees inasmuch as the fruiting bodies of many species are never found away from trees. Several such fungi are satellites of specific coniferous tree species (Romell, '21; Lange, '23). Cases are on record indicating that it is necessary for the mycorrhizal fungus to have access to living and functioning roots of the host tree. In one place where *Lactarius deliciosus* grew earlier, it was never seen again after the winter when the few spruces in the stand were cut (Romell, '30). A most striking result was observed in a trenching experiment made by the writer in a spruce forest in Sweden, more fully described elsewhere. In the year following the trenching, fruiting bodies of a number of fungi (chanterelles, cortinarii, lactarii, *Polyporus ovinus*) were seen crowded around the trenched areas, forming in places dense rows along the outer side of the trench, but inside of the trenches they were totally absent (Romell, '38). The same picture was seen the next summer (fig. 1).

Melin ('25) found in his culture experiments with isolated mycorrhizal

¹ Efforts have been made to evade even this assumption by postulating that the orchid takes up sugars or other energy-food directly from the soil where it is produced or made soluble by the fungus (cf., *c.g.*, Burges, '36). But nothing warrants this ecological application of Knudson's interesting physiological experiments; general experience in soil microbiology distinctly speaks against it (cf., in particular, Winogradsky's experiences with the "direct" method indicating that in the soil any easily utilized energy-yielding material must have very little chance of escaping the immediate mass attack of micro-organisms; for citations, see Romell, '36, p. 446).

fungi of trees that, in general, good growth was obtained only by using glucose or maltose as energy-food. He concluded that in nature the mycorrhizal fungi most probably take sugar from the tree roots. This idea is corroborated by the writer's trenching experiment. It should be carefully pointed out that the fungi crowding outside the trenches were not seen on any trenched area although some of these possess seedlings of spruce. This seems difficult to understand if we assume that the fungi are dependent upon their host for



FIG. 1. Detail from the trenching experiment (Romell, '38) in Orsa community forest, $61^{\circ} 25' 33''$ Lat. N., $14^{\circ} 52'$ Long. E. The strip of bare ground running from left below to the right top corner of the picture is an isolating trench (with a sheet-iron shielding, not visible) made 1936 in July. The ground seen in the lower right corner, covered with mosses and grass, is part of a trenched area where the blueberry bushes have been cut (as on about half of the trenched areas). Just outside the trench is a typical row of fruiting bodies of *Lactarius glycosmus*; the more distant ones are marked by pieces of white paper. This fungus has appeared thus far, in the same manner, around 7 out of the 31 trenched areas, but nowhere inside of a trench.—Author's photo, Sept. 10, 1938.

nothing other than for small amounts of vitamins, hormones, or similar additional nutrients, as has been suggested (cf. Romell, '38, for a somewhat fuller discussion).

Physiological and ecological experiments further indicate that the obligate mycorrhizal fungi of conifers are unable to cover their need of nitrogen food by decomposing soil organic matter. In Melin's pure-culture studies, ammonia was the only nitrogen compound which supported optimal growth with all species tested. Most other compounds tried, among which were peptone

and amino acids, were either worthless or served well for occasional species only. Cultures in forest humus studied by Hesselman and Melin ('27) have shown good development of mycorrhizas only in such humus where mineralized nitrogen is available. These results seem to be corroborated by Rayner's recent compost experiments.

Taking all the facts together, there seems to be scarcely an escape from the conclusions that the obligate mycorrhizal fungi associated to conifers are not saprophytes decomposing soil organic matter, and that they are energetically parasites on their host trees.

On the other hand, a number of striking instances are on record where conifers have failed to develop well unless associated to a mycorrhizal fungus (Oliveros, Rayner, and others; literature quoted by Hatch, '37; cf. also Rayner, '36). Such results have been obtained by Hatch using a soil as well supplied with nutrients as a prairie soil. The simplest explanation of this is no doubt found along Stahl's lines of reasoning (variously adopted, *e.g.*, by Müller, '03; Melin, '25; Hesselman, '26, p. 331 and 529; Romell, '35, p. 15; Hatch, '37), viz., assuming that the mycorrhizal hyphae take the place of roots and root-hairs.

The basis of the reciprocal relation thus existing between conifers and their mycorrhizal fungi can be pictured as follows, in close accordance with Stahl's views. For the trees with well developed assimilating systems, it is good business to yield some assimilates to associates building up, for the common good, a system of organs efficiently exploring the soil for essential nutrients. With the keen competition from the enormous masses of fungus hyphae in a typical softwood soil—for available nitrogen in particular, in a soil rich in slightly decomposed organic matter—an extraordinarily developed absorbing system is needed by the trees and the mycorrhizal hyphae are singularly suited for forming such a system. A mass of roots presenting the same surface and the same degree of omnipresence would seem to require a much greater expenditure of assimilates. If this is so, a sufficient root system would be more of a parasite on the tree than the mycorrhizal fungi are, and it is easy to realize how the mycorrhiza can be a "beneficial disease."

Looking at the matter from the standpoint of soil microbiology; the mycorrhizal hyphae are in a favored position as competitors for available nitrogen, etc., only as long as they are supplied with a source of energy particularly easily utilized. But if they are so supplied by the trees, their situation corresponds to that of the zymogenous soil microflora which, as is well known, by its intense competition is able virtually to exhaust the supply of available nitrogen in the soil when an easily utilized energy-yielding material is added in excess.

An interesting problem is the ecology of the chlorophyll-free *Monotropae* occurring in nature in a manner indicating them to be parasites on trees. The mycotrophic roots are entangled with hyphae and with tree mycorrhizas.

The most pertinent further information is no doubt Francke's ('34) finding that the fungus associated with *M. hypopitys* is a "sugar fungus" smelling like a *Boletus* and failing to grow on litter (leaves, needles) and on wood. Francke's culture experiments in *sterilized* soil are evidently irrelevant ecologically. His curious positive result growing his fungus on Merck's Acidum huminum and an earlier, often cited, occasional success in raising a monotropa away from trees scarcely contribute towards clearing up the ecological problem. These data neither explain nor agree with the manner in which the monotropas occur in nature, constantly following their apparent host plants² but occurring even where there is very little humus, as in dune sand (cf., e.g., Darbishire, '24, under 5:A:a, and Almqvist, '29, under *M. hypophegea*, p. 577). The writer ventures the hypothesis that the monotropas are energetically epiparasites on woody plants associated with the same fungus. This idea could be tested by trenching experiments.

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² It is true that the apparent host plants may vary, just as with mycorrhizal fungi. Darbishire's case of *Monotropa* associated to *Salix repens* (kindly brought to the writer's attention by Dr. M. C. Rayner) may be compared to *Lactarius deliciosus* occurring in other companionship than with spruce in North Africa (R. Maire, personal communication) and parts of Norway and of America, although being in Denmark (Lange), most of Sweden, and elsewhere, strictly a spruce satellite, or very nearly so.

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REACTIONS OF MUSKRAT POPULATIONS TO DROUGHT¹

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Field investigations of the muskrat (*Ondatra zibethica*) as part of a regular research program were begun in Iowa during the summer of 1934—a season of severe drought. Since then, drought periods of varying intensity and duration occurred in 1936 and 1937, although not all muskrat habitats under observation were similarly or contemporaneously affected.

The principal data on reactions of muskrats to drought were secured from 5.5 to 11.0 miles³ of Squaw Creek, 1.0 to 2.8 miles of Skunk River, and 2.2 to 2.6 miles of small streams in Story and Boone Counties, 1934, 1936-'38; Little Wall Lake, a marsh of 230 acres in Hamilton Co., 1936-'38; various marshes and potholes in Clay and Palo Alto Counties, in the general vicinity of Ruthven, 1936-'37. The work in the Ruthven area was done largely on Round Lake, a state-owned marsh and wildlife refuge of about 450 acres; potholes in the state-owned 392 acre waterfowl breeding ground known as Dewey's Pasture; and Mud Lake, of which about 300 acres of privately owned marsh were made available for study through the courtesy of the Mud Lake Fur Farm.

Less intensive studies were made in other Iowa localities, and the Iowa data are further supplemented by notes taken in South Dakota as a fur trapper between 1919 and 1928 and in connection with irregular inspections of familiar muskrat habitats or former habitats, 1930-'37. Except in habitats associated with the larger lakes and rivers, muskrats have been observed during dry years in most types of environment usually occupied in the prairie region of north-central United States.

ADAPTATIONS OF THE MUSKRAT FOR EXISTENCE

The muskrat is such a common mammal and its geographic range—both native and acquired—is so great (Storer, '37) that a detailed description of it should not be necessary in this paper.

Hindfeet and tail of the animal are efficient organs for swimming, and it is, within limits (Errington, '37d), well suited to a semi-aquatic life. It finds optimum living conditions in places where heavy growths of herbaceous

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² Iowa State College in cooperation with the U. S. Biological Survey, the American Wildlife Institute, and the Iowa Conservation Commission.

³ Calculations of lengths of watercourses neglect minor windings of channels and refer to minimum and maximum distances under observation during the drought studies.

vegetation occur in close proximity to still or sluggish water that fluctuates neither suddenly nor greatly in depth.

The muskrat, nevertheless, may be surprisingly adaptable to habitat changes, some of which may be quite adverse. Its will to live may not in actuality be stronger than that of many other species, wild or domesticated, but such may be manifested in pronounced ways. A cornered muskrat (or one that may sense that it is cornered) is a notoriously desperate fighter, attacking man (Johnson, '25, p. 287; Seton, '29, pp. 594-596), livestock, or even moving inanimate objects on sight. It may engage in vicious intra-specific strife or cannibalism. When it has to, it may eat nearly any natural organic matter, including wood; it may adhere to hazardous routines of feeding or foraging; and whether it remains tenaciously in drought-exposed burrows of its accustomed home range or establishes itself in a farm yard or in a small-town vegetable cellar, its conspicuous objective is to continue living, by any means within its power.

The muskrat's physical limits of tolerance to vicissitudes of drought are hard to evaluate because of the variables usually entering the equation. Adults seemingly may maintain themselves for weeks in hot weather without water except that which they get from moist foods, but field evidence suggests that young animals of post-weaning to half-grown sizes may die of thirst under similar conditions. The muskrat seems to be remarkably efficient in the digestion and assimilation of harsh food such as dry corn stalks and coarse, dead, weedy growths to which it may resort, when pressed, though how much nutriment the animals actually receive from this sort of material is questionable.

Musk rats cannot withstand much direct exposure to severe cold or freezing wind; and the drying up of their habitats tremendously increases their vulnerability to mink (*Mustela vison*), red foxes (*Vulpes* spp.), dogs (*Canis familiaris*), and other enemies. On land, they are easily discovered and easily approached and, for all of their militant behavior and the sharpness of their incisors, are neither agile enough to escape nor formidable enough to fight off attackers from which they would normally have much less to fear.

ATTACHMENT OF MUSKRATS FOR HOME RANGES

Field observations as well as tagging studies (Errington and Errington, '37) suggest that the muskrat's individual home range is typically rather limited in area. While evidence of a certain amount of overlapping of home ranges and common occupancy of lodges and burrow systems may be seen, the tendency appears to be for muskrats to remain in much the same sections of a given marsh or stream during summer, fall, and winter.

Activities within an established home range are somewhat routinized and seem strongly influenced by the size and shape of the range, the situation as concerns food, cover, and water, and relations between muskrats in adjoining or co-occupied ranges.

Observed home ranges of muskrats on Mud and Round Lakes tended to be more nearly circular toward the centers of the marshes than the shore ranges, the latter of which were often rather narrow strips extending from bank burrows out into deeper water for several hundred feet. Occupants of these strip-shaped ranges may, with the approach of winter or the recession of water in mid-summer, move considerable distances into the marsh and still not become involved with other muskrats' "property rights."

Thirteen young muskrats tagged on Round Lake during the summer of 1936 were recovered in fall and early winter following. Three of these were captured in May and June, tagged, and released at once in natal localities that were closely bounded on all sides either by occupied ranges or unfavorable environment; they were taken by the Conservation Commission for specimens in November and December at an average distance of about 70 yards from their sites of tagging and release. Nine others, all captured for tagging in elongated ranges or in relatively muskrat-vacant habitats, were similarly recovered during the State trapping (Errington and Errington, '37) but at an average distance of about 280 yards from sites of tagging, seven having been recovered nearly straight out in the marsh from where tagged. The thirteenth evidently took to wandering in late summer or fall, as it was reported trapped in a drainage ditch about four miles from the site of tagging. One other young animal was tagged June 15, 1935, near the south shore of Mud Lake in an elongated range and was caught by a trapper January 2, 1936, about 200 yards out in the marsh.

Some actual range extension has been observed. In early summer, 1935, the breeding population on an area of 41.5 acres in the northeast corner of Round Lake was calculated at 30 pairs on the basis of distribution of known litters in 48 habitable lodges. Vegetation of types furnishing muskrat-favored food and building material was sparse here, and a mid-summer sinking of the water level of about seven inches from late June to late July further decreased the attractiveness of the area for resident muskrats. From 200 to 300 yards out in the marsh, however, not only was the water of more satisfactory depth and densely grown over with rushes, but there were practically no muskrats occupying an area of perhaps 20 acres. It became readily apparent in early July that adults and active sizes of young were gradually moving deeper into the marsh, building flimsy nests as they went (Errington, '37d). The breeding season was largely over by July 23 (Errington, '37c), at which time the centripetal drift of adults and young was most pronounced; by August 3, most of the population was living in the heavier rush growths from 300 to 400 yards from shore; and by August 27, there were only 12 lodges remaining in the old area that showed current sign of use. Of the latter 12 lodges, six had either been well situated in the first place or shut off from better habitat by a wide zone of continuously occupied ranges.

The drift described in the preceding paragraph was in many ways comparable to late summer and fall adjustments within elongated shore-to-deep

water home ranges. Although it is exceedingly probable that many of the muskrats stationed themselves in wintering grounds completely outside of their spring and early summer home ranges, the drift was of the nature of mass extension of ranges into a portion of the marsh that was essentially virgin habitat.

Aside from imperfectly understood spring movements associated with the breeding season, sporadic drifting of both sexes may take place throughout the year when neither overcrowding nor unfavorable living conditions seem to be underlying causes. Once the animals leave familiar territory, there seems to be no predicting where they will go. Tagging data (Errington and Errington, '37, and unpublished) have shown recoveries of departed individuals at distances of three to 21 miles from sites of tagging and former residence, and wandering muskrats tracked in snow (but not disturbed) have covered as much as 2800 yards in about a half day.

MUSKRAT HOME RANGES AND MOVEMENT DURING DROUGHT PERIODS

Muskrat behavior during droughts follows much the same patterns that it does at other times except for modification or accentuation as the stimulus of danger or necessity becomes increasingly acute. As habitats go dry, varying degrees of attachment of muskrats for their home ranges and accustomed quarters may be observed. Most of the animals remain where already established, though what they do may depend to some extent upon the season of the year, fall representing a time when less attractive ranges seem most likely to be abandoned.

In one of the first Dewey's Pasture potholes to go dry in 1936, the visible water disappeared about the middle of June; muskrats were active in local habitats from July 6 to July 26 but apparently none were left by August 1. Other potholes went dry in late June and early July and in these there was still much evidence of occupancy about the main lodges and bank burrows by July 15; by July 30 few muskrats remained. Of two large potholes in Dewey's Pasture that had just gone dry by July 30, one had no muskrats by August 31 but in the other recent evidence of muskrats maintaining themselves was seen as late as October 19.

The periods of conspicuous occupancy after disappearance of the visible water—from three to 11 weeks—seemed to vary mainly with the length of time that the residents could stay alive, although many animals simply departed. In all cases, the heaviest "sign" was consistently localized either about old habitations or in especially dense stands of rush or grassy vegetation. The shallow marsh west of Ruthven known as Whitford's Slough, which went dry in early July, was examined on July 27; much less "sign" was found about lodges than in growths of bulrush (*Scirpus* spp.) and other dense marshy vegetation forming canopies under which the muskrats were living somewhat like rabbits.

As large marshes go dry, considerable local shifting of population centers

may take place in lightly populated areas. Seven muskrat family groups were judged to be the resident population of the tract of about 90 acres of Little Wall Lake that was habitable during the summer of 1937; and the foci of activity of these, with one exception, were distributed rather uniformly 200 yards or more apart. The marsh was practically dry by September, at which time evidence of regular use was to be seen only in the vicinity of the summer habitats. By late October, two of the original home ranges on one side of the 90 acre area had been abandoned with no evidence that the animals had stayed on the marsh; two original ranges in the center continued to be in use; and the animals of the other three ranges had moved into a common area, previously nearly vacant. Into the latter area had converged by the November trapping season virtually the entire muskrat population—16 individuals, as reported by trappers who evidently caught all.

The movement took place in easy stages and usually through extension of trails away from the breeding lodges into new territory. Temporary lodges were sometimes built enroute at varying distances from the old ones; then, from these, other trail systems became established, the animals ultimately living hundreds of yards from their summer quarters. Even so, however, trails between new ranges and old showed continued if diminishing travel for weeks, which further illustrates the gradualness in change of routines of individuals remaining in familiar surroundings.

Muskrat occupants of sparsely populated drying stream beds may also change their living routines gradually. Indicative of the manner of adjustment are some 1937 notes from Squaw Creek. One muskrat evidently "commuted" for several days in late August over a stretch of about 600 yards of exposed stream bed before it finally abandoned its old pothole for a more attractive one having, however, muskrats already in residence. An acceleration of local movement within the supposed radius of familiarity of resident animals generally seems to precede shifts in living quarters.

It sometimes happens that muskrats may be fatally slow in making adjustments even when superior habitats exist in their home ranges. In three of four areas about Round Lake where local populations were consistently bank-dwelling in 1936, the residents lost severely from mink through remaining in exposed burrows, although they were frequenting more and more a number of feeding rafts and freshly-built temporary lodges in the rushy growths out in the marsh where the water was fairly deep. In the fourth area, the water did not recede sufficiently to expose the burrows, and the occupants continued to live there without detected losses during the summer.

The 1936 late fall population on Little Wall Lake was calculated at about 40 individuals in an area of about 100 acres. A smaller area a few hundred yards to the side went dry and was depopulated in summer and early fall, but it is not believed that many of the muskrats from here stationed themselves in the 100 acre tract. In the latter area, the principal "sign" in late fall continued to be seen about lodges steadily used during the summer.

Similarly, the eastern part of Mud Lake dried up in the summer and fall of 1936, and well-used habitats were consistently occupied despite far more favorable food and water conditions in wetter and intervening—but already occupied—portions of the marsh. Trapping in November revealed a population density between two and three muskrats per acre in the wet marsh and a population of about one muskrat per acre on adjacent land that had not been covered with water for at least a month. Furthermore, only a very small proportion of the animals trapped in the better grades of habitats showed the poor flesh and wounds often indicative of trespassers. A few occupied ranges were still to be found as late as November 4 nearly a quarter of a mile from water-covered parts of Mud Lake and in places that had almost certainly been exposed since early September.

About streams and marshes alike, it appears broadly true that the most complex and long established burrow systems are the ones likely to continue in use to the last (Errington, '37b). When dried out muskrat habitations no longer show evidence of occupancy, animals may still be living not far away in woodchuck holes, cornfields, etc., in range that is patently familiar to them, and, at least in some cases, may reoccupy the old burrows after the return of water.

Fall drifting of individual muskrats occurs so much in "normal" years that one has difficulty dissociating it from movements due to drought eviction. It is apparent, nevertheless, that final abandonment of familiar habitats on the part of a great many muskrats is a desperate forerunner to what may be still more desperate eventuality.

INTRASPECIFIC STRIFE

It is well known that muskrats may live in crowded quarters, Bailey ('37) stating that, "Sometimes 10, 20, or 30 muskrats have been found in one of the bank burrows in winter when they were being mercilessly trapped in the marshes. . . ." Well known also is the propensity of males to fight among themselves in the breeding season and the killing of trapped muskrats by other individuals, though, on the whole, the animals are not considered unsociable.

Recent Iowa studies, however, have brought out evidence of a tremendous amount of natural friction in muskrat populations, this ranging from mere displays of ill temper to lethal attacks and involving both sexes of old or young at all seasons of the year.

Apart from spring fighting, which seems chiefly a manifestation of sexual unrest and aggression, the most vicious strife recorded has been in fall and winter during periods of population adjustment. Insofar as drought conditions may be followed by abandonment of home ranges by an unknown but surely substantial proportion of the muskrats in a given locality, the resulting increase of habitat-seeking animals may be expected to intensify existing population tensions. It is doubtless true that the wandering of some indi-

viduals may be so haphazard and their routes of travel beset by so many dangers that a large number may never again encounter their own kind; but with the aid of tracking snows an investigator may often find evidence of wanderers trickling in or out of the last few occupied habitats. The occupied habitats may themselves not only be filled to their apparent capacity but may also be losing their habitability for the animals already resident.

Fall and winter advent of newcomers into well-populated habitats generally seems to mean trouble. At times, mutual antagonism of residents and newcomers appears but a consequence of strangers meeting, and the newcomer may continue on its way or conceivably remain in the vicinity until tolerated or accepted. But when invader meets resident in the tunnel system of one of last lodges to be used in a dry marsh, conflict may be indeed savage.

Five muskrats wandering on Round Lake between November 5 and 8, 1936, were examined. These were two adult females and two females and one male of the year. All were thin and all showed fresh or recently healed wounds of the types administered by fighting muskrats. One had died of wounds a short time before it was found; and another had a probably fatal wound in the back through which putrid intestinal contents had penetrated. Six muskrats taken by trappers on November 11 from the dry eastern end of Mud Lake, about three miles distant from Round Lake, were likewise examined: three adult females, one adult male, and one female and one male of the year. These were as thin and as chewed up as the Round Lake specimens; one had a wound in the back exposing part of its intestines. One of the trappers wrote that he would judge 90 per cent of the muskrat pelts taken from dry marsh were damaged (Verl Black, letter, November 16, 1936).

Snow trails of other wanderers followed on frozen Round and Mud Lakes in November, 1936, revealed more evidence of erratic movement by a limited number of muskrats, very probably of animals abandoning uncongenial habitats as those observed about the dry portions of Mud Lake. The animals would rest in flimsy nests improvised on top of the ice from shredded dry vegetation or spend a few hours in lodges entered by means of open water, only to move on and perhaps leave blood-marked trails leading away from the marshes.

The smaller streams in Central Iowa went dry in the summer of 1934 and 1936 and the summer and fall of 1937 to the extent that nearly all of the muskrats remaining in residence became concentrated in a few residual potholes. There was no evidence of any large number occupying any particular pothole—seldom more than four or five by fall and usually only one or two.

No data from examination of muskrats taken from the Squaw Creek potholes are at hand, but, in the winter of 1924–25, I trapped muskrats in potholes of similar nature in a creek bed in Haakon Co., western South Dakota. Here, the muskrat-occupied potholes were small (averaging possibly about 1500 square feet water surface and about 2.5 feet center depth),

obviously short of readily available food, and the animals fed chiefly on vegetation of surrounding land until the potholes were sealed by ice. Trapping yielded about one muskrat per pothole, although six were caught in one narrow body of water that was about 100 yards in length. My December catch of 149 pelts was badly damaged, and notes indicate that about half of the pelts showed major wounds in all stages of healing, nearly all of which may be attributed to wholly expected intraspecific strife.

Crowding of muskrats into small water holes is not always attended by severe friction, however. During the summer of 1937, there were only scattered puddles of water in the bed of the drainage ditch near Story City, and the muskrat population was localized by November in two sets of burrows having hardly sufficient water to cover the entrances. Trappers took seven out of one set of burrows and about 20 out of the other. Of 39 muskrats trapped from this ditch that were examined—including most of those from the half mile under observation—only one was conspicuously in poor condition and that may have been a wanderer. The muskrats were living amid an abundance of corn and other excellent food, which doubtless mitigated some of the evils and irritations of congestion.

PREDATION

In many respects, the conditions accelerating muskrat losses from predatory enemies are the same as those under which intraspecific strife increases. Predation may actually be intraspecific, though cannibalism in the muskrat is more often a matter of one animal dying or being killed by another and later fed upon as a cold carcass. This was of rather frequent occurrence in densely populated sections of Round and Mud Lakes in 1935; but was also conspicuous in sparsely populated Dewey's Pasture potholes and Little Wall Lake when they were going dry in 1936 and 1937, respectively. Partly grown young seem most likely to be killed and ultimately eaten by larger young or by adults.

An instance of possibly direct intraspecific predation by one adult muskrat upon another on dried up Little Wall Lake may be briefly described. On December 8, 1936, a large muskrat, losing considerable blood, left a regularly used lodge from which it apparently had been driven after entering as a wanderer. It travelled about 175 yards and entered another lodge. Late in the afternoon of the next day, it left this lodge and followed the shoreline for approximately one mile, taking refuge in a drift-covered weed patch on the opposite side of the marsh. Just outside of the lodge it had left were remains of a freshly dead muskrat, and two fecal passages picked up in the trail of the wanderer consisted of muskrat fur. A uniformity of previous foraging routes in the vicinity of the invaded lodge suggests that the partly eaten muskrat had been an established occupant. Conditions for tracking and "reading of sign" were very favorable.

Data showing increased pressure upon muskrats by the red fox during the drought of 1934 have been presented (Errington, '37a), but our data on mink food habits in relation to population phenomena of muskrats are still in unpublished and largely unorganized state. The effect of drought on vulnerability of muskrats to mink is so pronounced, nevertheless, that a few examples should be appropriate in this paper.

For both summers of 1936 and 1937 there were on Round Lake close to one adult muskrat per 2.7 acres and in both years the spring mortality from mink was conspicuous. In 1936, the mink pressure slackened in May but was resumed in July as the water level of the marsh went down. Exposure of the bank burrows along about 300 yards of the southeast shore was followed by the killing by mink, largely between July 22 and August 1, of apparently all but one of eight muskrats believed to be resident there. The one individual known to have escaped was living in a newly built lodge about 60 yards from shore. Similar mortality in other exposed shore habitats was also detected but nearly the entire population of Round Lake was already living in much greater security in lodges deeper in the marsh. In contrast, the summer of 1937 was a season of high water in northwest Iowa, and examination of mink prey items and 168 fecal passages gathered from Round Lake did not disclose any evidence of mink pressure upon muskrats from May to early October.

The vulnerability of the muskrats of the Dewey's Pasture potholes, which went dry from June to August, 1936, seemed to become critical just after the disappearance of the surface water. Mink feces deposited before this time rarely contained muskrat remains; then, with the exposure of the muskrats, mink diet ran strongly to this item for a week or two; and, finally, with the majority of the muskrats dead or departed, the mink turned to other prey types, often land forms as ground squirrels (*Citellus* spp.) and insects. Subsequent to the short period of acute vulnerability, muskrat remains occurred in mink feces only occasionally, even when fairly substantial remnants of muskrat populations still occupied their old quarters for weeks afterward. Continued survival of immature, diseased, and otherwise handicapped individuals hints that the lessening of mink pressure may to some extent be due to mink not happening to encounter remaining muskrats with frequency; certain muskrats, however, obviously form safer habits and occupy better quarters than others, and there is increasing evidence that meeting with a mink does not always result in death—especially if the muskrat is large and the mink small.

The role of mink pressure *per se* in contributing to the decline of muskrat populations during drought is by no means clear, as may be illustrated by the 1937 summer and fall data from Squaw Creek. In September, several sets of dried out runways and burrows, which had been used by muskrats for weeks despite much mink activity in the vicinity, became gradually depopulated, but only four of 90 mink fecal passages collected along this creek

contained muskrat remains. The muskrat representations in the mink feces were of different individuals of which three were determined with fair certainty to have been killed in or near habitats still having considerable water. Two of the four muskrat-containing passages were picked up beside a small pothole in which muskrats tended to concentrate, trappers having caught five here in November and two more in land holes near by.

Dearborn ('32) found food in 297 stomachs of Michigan mink taken during the 1930-31 trapping season and gives 65.92 per cent as the frequency index of the muskrat in winter diet. Errington and Kenneth Krumm have unpublished data from the upper Missouri Valley States that show a correspondingly high incidence of muskrat remains in local collections of winter mink feces, but, in "normal" years, muskrats are seldom represented so heavily in mink diet unless living at high densities. During drought crises, representation may be equally high when muskrat densities may be low; though, even when remnants of muskrat populations may be wintering under conditions subjecting them to severe predation and dooming them to annihilation before spring, it does not necessarily follow that the predation itself is annihilative or has significant net effect on the fate of the animals.

Of the calculated late fall population of muskrats on Little Wall Lake in 1936, perhaps a dozen were suspected of having been removed from one part of the marsh through illegal trapping in December and three others were collected for specimens. No indications of any of the original winter residents being alive were seen after February 4, 1937. Twenty-one of 41 mink fecal passages gathered between December 5 and February 23 contained muskrat remains. Thirteen carcasses of muskrats dying in this period were found; one was killed by a mink, one positively and another probably by other muskrats, and, while the carcasses of 10 others were too fragmentary to reveal satisfactorily the immediate causes of death, the likelihood is that mortality occurred not only from predation and intraspecific strife but also from mid-winter hunger and cold.

Three muskrats were known definitely to have left Little Wall Lake during December and January, 1936-'37, but there was no way of determining whether they had been residents up to that time or had wandered into the area some days previously. It is believed that the greater part of the Little Wall Lake winter decline not otherwise accounted for was due to egress, and this in turn probably meant death for most animals from factors other than predation.

FOODS AND FEEDING ROUTINES

What a muskrat population eats is in large measure determined by relative availability of foods and by established feeding habits. Some populations may be so herbivorous that it is difficult to find evidence of any animal foods at all in their diets; others may be so carnivorous that their ordinary diets of frogs, fish, and molluscs may differ only slightly from those of mink

frequenting the same areas. These differences may be considered of normal occurrence, and drought, under conditions observed, did not bring about pronounced departures in feeding tendencies except through actual crisis. Even then, changes were often changes only in degree; the finding of muskrat remains in quantity in four of 16 muskrat stomachs and fecal passages collected on Little Wall Lake in the winter of 1936-37 was foreshadowed by cannibalistic traits shown by the muskrats of Mud and Round Lakes during non-crisis seasons; the feeding of drought-exposed muskrats on dry corn stalks and dead weeds in winter has its counterpart in the usual diet of many individuals wintering in flowing central Iowa streams (Errington, '37b, and unpublished).

But muskrat feeding routines may be tremendously affected by drought as food sources become difficultly accessible or accessible only at increasing peril, although for a time muskrats forced by drought to forage extensively on dry land may find themselves living at no greater disadvantage than many ditch-dwelling muskrats commonly do. As the water table in a marsh descends below the level to which the muskrats deepen their burrows, however, the animals become more dependent upon food as a source of water for body requirements; moisture-containing foods—rootstocks, tubers, corms, etc., of cat-tail (*Typha* spp.), Cyperaceae, Iridaceae, Compositae—must perhaps be dug from dry or hardened ground if the muskrats are to remain alive in their habitats.

Freezing of exposed marsh bottoms in late fall plainly restricts foraging activities of muskrats resident there. At first, cat-tail or rush underparts may still be found in sheltered places where the mud is unfrozen; the animals may later have to chew their way through a frozen crust to reach the more succulent types of food; and, finally, they may find it so difficult to chew down through both frozen ground and an upper accumulation of ice and hard snow that they no longer try, contenting themselves with what food they may discover above ground. Heavy accumulations of snow may prevent some feeding areas from freezing deeply.

Winter foods eaten by muskrats residing in dry marshes and stream beds may be coarse fodder, indeed, but, as indicated, surely not a great deal more innutritious than foods to which muskrats better situated with respect to water may have to resort. Stems and down of cat-tails, tops of bulrushes, leaves and stalks of corn in fields, bare corn cobs, dead grass and weeds, all dry and weathered or water-soaked and half-rotten, are the main items of winter diet for many Iowa muskrats, whether drought conditions prevail or whether they do not. Muskrats are not thought to maintain weight indefinitely on this sort of fare but appear able to survive the winter on it, specially if they supplement their diet on occasion with foods of superior nutritive quality, such as ear corn or flesh.

At least some of the critical aspects of the food situation for muskrats wintering in a dry marsh may be due to exposure to cold and energy-con-

suming activities necessitated by the freezing of the ground. The population on Little Wall Lake in the winter of 1936-37 fed chiefly on cat-tail growths that could be reached only from above, but the animals spent most of their time in their lodges or tunnels and kept the passages to the outside well plugged with mud or wet vegetation when not actually using them, the plugs in the course of hours freezing solidly. During December and January, individual muskrats gnawed through icy mud nearly every day just to emerge from their underground quarters and, once in the cat-tails, not infrequently did extensive cutting and digging without always finding much to eat. Upon returning to its quarters after feeding, a muskrat sometimes found that the passageway had been plugged by another occupant. In one recorded instance an animal thus "locked out" was encountered in late afternoon, December 4, 1937, as it was sitting beside a small hole it had cut in a crack over a tunnel near its lodge; it still had 12 to 15 cubic inches of frozen mud to remove before it could enter. Collected for a specimen, this individual proved to be a female of the year, lean but in good condition, and had fed on cat-tail rootstalk and associated material.

In only one small area of Little Wall Lake where about a foot of ice covered the bottom was evidence seen that muskrats were consistently staying in their burrows; elsewhere on the marsh, the entire population seemed sooner or later to forage on the surface, although not always with regularity. Some muskrats were known to have had access to carcasses inside of their habitations, and, since outside foragers were rarely noted to feed upon anything except vegetable matter, the greater part of the carcass-feeding revealed by stomach and fecal contents must have taken place in sub-surface retreats. Not only did muskrats feed upon carcasses of their own kind but on cottontail rabbit (*Sylvilagus floridanus*) and Bell's painted turtle (*Chrysemys picta bellii*).

Muskrats that were worked with typically wintered under the ice if it was of substantial thickness and if the sub-surface food supply remained ample and accessible, even when the water of a marsh, pothole, or stream froze to the bottom. The maximum depth of water in Round Lake was only about 1.5 feet by early winter, 1936-37, and the frost-line sank beyond this before the winter was over; nevertheless, the muskrat survival rate was comparatively high. Breaking out of sub-surface retreats by the muskrats and subsequent hazardous activities seem most likely to occur either when little food exists under the ice at all (as in many potholes in small stream beds) or when the water over the marsh bottom is so shallow that not only does it freeze but also a foot or more of the mud below, including matrix containing cat-tail rootstocks and similar important foods.

As a habitat goes dry in fall, muskrats remaining are far more particular to establish winter quarters in those portions of their home ranges having a good food supply than in places having perhaps more water but scant food. In the event that they make an opposite choice, they may later leave their

deep-water habitats daily to travel hundreds of yards to and from their feeding grounds over exposed routes.

The established way of living of muskrat populations may also have a bearing upon how the animals meet the problem of winter feeding in dry or nearly dry environment. Marsh-dwelling muskrats, obtaining their food from the marsh largely as required each day, seldom appear to develop storage habits; accordingly, when attempting to continue their usual feeding routines under drought conditions, they may find themselves confronted by crises that exceed their immediate adaptability. Conversely, many ditch-dwelling populations in central Iowa regularly carry large quantities of ear corn, dry grass, and other edible material into their burrows in fall and, not being forced to seek food outside, may winter at high densities in quarters that are very restricted and almost as water-less as some of those in dried up marshes.

Much outside activity of stream-dwelling muskrats in winter is plainly due to animals establishing themselves in new quarters too late in the fall to make adequate preparations for cold weather. For example, by autumn, 1937, some water had returned to a previously dry stretch of Squaw Creek, and, in late October, a muskrat moved in and dug a set of burrows. It foraged regularly on land near by until the following January, long after muskrats in better situations along the creek had ceased to come out. With a gradual rise in water during mid-winter, the muskrat at this place came out less frequently and finally did all of its known foraging on bank vegetation now available under cover of the ice.

Muskrats are encountered living in corn cribs, corn shocks, and other food-rich land retreats, but I have never found clear evidence that they actually succeed in wintering there in states having rigorous winter climate. I have a field note dated December 4, 1927, relating to a muskrat in a wire corn crib on a farm in Brookings County, South Dakota; at this date, it had been there for many days and had dug into the crib at ground level for about two feet; its tail was frozen, however, and it stayed less than a week longer, probably wandering off to die.

DIGGING AND BUILDING

Many of Johnson's ('25) observations on muskrat marshes in New York were made during the drier summer months, and for general information on lodge construction, burrowing, etc., the reader may be referred to pages 261-278. Much of the Iowa research dealt with situations that became progressively critical, and changes in living quarters followed rather definite sequences, some of which may be outlined in the present paper.

As entrances to lodges and bank burrows become exposed, muskrats usually deepen the passageways, though seldom to a depth greater than 18 inches below their former level. Deepening may take the form of simple

excavations or of complex channel systems radiating finger-like away from the entrances which in most cases contain the last visible water. Accelerated digging may be noted in summer at about the time when residual puddles assume the consistency of liquid mud; also, in late fall, after the first heavy frosts, though a comparatively large amount of water may still be left in the entrances. Digging at "freeze-up" is especially apt to take place on an extensive scale and to show the most variation; mud and peat may be piled at the ends and sides of ramifying channels; wide, straight canals may be cut down below the water level, extended for yards, and then used no more; pockets and blind burrows may be dug from the surface and enlarged in underground feeding areas amid the rootstocks of water plants.

Old lodges continue to be favorite retreats during drought, both in summer and winter, but often the original chambers are abandoned in favor of new ones hollowed out below. The muskrats may enter and leave the dry lodges through holes at the lower edges or tunnel openings a few feet or yards way. Sometimes, they will use holes in the tops or sides of the lodges comparable to, or the same as, those made by invading mink.

Along shores, new sets of burrows may be dug under the old as the water goes down, but, if the soil is gravelly, frozen, or otherwise resistant to digging, the muskrats may be content to try to keep their old burrows habitable by much plugging with available materials.

Lodges may be newly constructed of plastered mud and vegetation as the water of marshes recedes in summer or fall and, while these are usually to be found a short distance out from shore, they may also be built wherever needed. In building a new lodge on exposed marsh bottom, the muskrats simply cut away the most convenient heavy vegetation (cat-tails, *Cyperaceae*, etc.) and pile it in the center of the cleared space. The resulting structure may cover previously existing channels and burrows, but more often the digging is done later, when the structure is being hollowed and otherwise modified for use. The technique of building a corn field lodge is similar, except that corn stalks and field debris are used instead of mixtures of marsh material.

Practically anything that is portable may be used in building or repair work—marsh plants, grasses, weeds, willow shoots, sticks, roots, corn cobs, bones, pieces of heavy bark, stones, clam shells—and these may be stuffed into openings under root-tangles of waterside trees, made into flimsy canopies over burrow entrances, or heaped or plugged according to the needs or impulses of the muskrats.

If winter comes when a muskrat-occupied marsh is dry or has only a few inches of water over the mud bottom, the existing burrows may continue in use as retreats and passageways and there may be additional sub-surface tunnelling in unfrozen strata of ground, but, as previously indicated, the muskrats tend to seek their food outside. When the weather is extremely

cold and the ground unprotected by snow, foraging muskrats may not succeed in plugging completely the burrow or lodge openings used in passage, presumably because of scarcity of available unfrozen mud. On the several occasions when this was noted at Little Wall Lake in the winter of 1936-37, death of the occupants appeared to follow promptly.

During winters accompanied by deeply drifted snow, the muskrat situation in a dry marsh may be less critical. Drifts may accumulate to depths of many feet over the cat-tails, reeds, and Cyperaceae and may often be filled with muskrat tunnels and nests; and, where the drifts are extensive, muskrats may live in them for weeks without coming out in the open, quickly plugging with vegetation breaks made accidentally or by mink.

If the water of a marsh is perhaps a foot in depth when it freezes, the muskrats may sink channels into the underlying mud, which, along with burrow systems, may be used as retreats as well as passageways. Persons illegally spearing muskrats through the lodges on Round Lake in the winter of 1936-37 were said to have had poor success; and, as a strong population survived despite the low water level, it may be inferred that the animals were not staying in the lodges nearly to the extent that they ordinarily do.

In mid-winter, 1919-20, I did some trapping west of Brookings, South Dakota, about a long, open marsh having a small number of muskrats resident in bank burrows. The water and mud alike had frozen to a depth of about two feet, but the underground passageways at this level were still travelled. One runway was chopped open for a short distance and found to have soft mud at the bottom and to show evidence of having been gradually deepened as the frost-line descended.

DROUGHT MORTALITY

The variable introduced by egress of muskrats from dried out habitats of course increases the difficulty of evaluating drought mortality, even when some measurement of the decline of a local population may be made. This is particularly true when little actual evidence of mortality may be found and when some muskrats may be known to be establishing themselves in new quarters or congregating in areas remaining habitable. The evidence indicates, however, that in north-central states but a minor proportion of drought-evicted muskrats find any sort of safety.

In late summer and early fall, 1937, an unbroken stretch comprising over half of the 7.7 miles of Squaw Creek under observation became depopulated. That this decline was accompanied by slight increase of the animals in occupied potholes is suggested by trappers reporting a catch of only 10 muskrats (two of which were living in holes in high ground) from nearly two miles of creek having the strongest populations remaining. The catch of 10 muskrats represented all but one known to have been alive along approximately five miles of creek and in environment that could reasonably have been ex-

pected to yield an average of at least 10 per mile had it not been for the year's drought.

The data on decline of the muskrat populations of the Dewey's Pasture potholes in 1936 are not complete enough to permit numerical estimates of the losses, but much evidence of mortality was found in the lodges and through examination of mink feces. Comparison of trappers' catches on wet and dry portions of Mud Lake, on the other hand, may provide a useful index.

Of the 300 acres of marsh controlled by the Mud Lake Fur Farm, probably about 100 acres were dry by fall, 1936. The season's catch was 501 muskrats (letter, Joe Kautzky, Jr., March 23, 1938), of which 42 were reported taken from dry marsh (letter, John Garlisch, November 17, 1936). It is believed that practically the entire population was caught, which would give a November density close to 459 muskrats on about 200 acres of wet marsh, compared to 42 on the total of 100 acres that had dried up since summer and of which only about 40 acres were still muskrat-occupied by the trapping season. The fall population of 2.3 animals per acre for wet marsh apparently had not been significantly affected by the drought; and, on a pro-rata basis, a reduction on the dry marsh to less than one-half muskrat per acre would mean a net lowering of the population density of Mud Lake Fur Farm's 300 acres by almost 200 individuals.

By analogy, the very similar Little Wall Lake population, which in late fall, 1936, was calculated at about 40 individuals on about 100 acres, may also have been reduced by about 200 through drought, but here it is suspected that the losses were heavier. The possibility of epidemic disease entering the picture is suggested by the finding on October 27 in one area of about 1400 square feet of five decayed but otherwise nearly intact carcasses of adult muskrats that had died some weeks previously.

For 1937, the summer and fall losses on Little Wall Lake that may be attributed to drought were likewise severe. The 16 muskrats taken by trappers in November were the remnant of a breeding population of at least seven females and associated males plus their offspring in 13 known litters.

Little of the summer drought loss recorded in the Iowa studies appears to have been due to shortening of the muskrat breeding season. The mid-summer drying up of the Dewey's Pasture potholes in 1936 doubtless cut down the number of litters born, but as long as shallow surface water remains in a habitat—as it commonly does until the breeding season is essentially over—mating and giving birth to and suckling of litters may go on much as usual. The seasonal distribution of litters in northwest Iowa was about the same during both the wet summer of 1935 and the drought summer of 1936 (Errington, '37c).

The net productivity of the breeding population of Round Lake was greater in 1937 than in 1936, however. The age ratios of muskrats collected

by the Conservation Commission in late fall and early winter were 2.69 young per adult for 181 specimens in 1936 and 3.73 young per adult for 208 specimens in 1937. In this case, the higher water level in 1937 was judged to have given the population (breeding density was about the same as that of 1936) increased protection from mink, but it may also have reduced losses from diseases the spread of which may be aided by low water. On the other hand, the highest rate of increase indicated by my notes—an age ratio of 6.8 young per adult for 39 November, 1937, specimens—was recorded for the drainage ditch habitat near Story City, in which the water throughout most of the summer was muddy, stagnant, and hardly sufficient in quantity to cover the burrow entrances.

Winter may bring but a continuation or completion of the drought mortality begun in warm weather, as in 1936–37 on Little Wall Lake, where the last wintering muskrat had died or disappeared by early February; or it may mean the beginning of unendurable crisis for populations that had been faring passably well under less adverse conditions of summer and fall.

An index of mortality suffered by muskrats wintering in nearly foodless small stream bed potholes is afforded by 1924–25 notes taken while trapping in Haakon County, South Dakota. Pre-trapping reconnaissance of two creeks indicated that the fall muskrat population was about the same on each and similarly distributed. Only one creek was trapped but that severely, all known trappers taking slightly over 160 muskrats from about six miles of potholes or probably close to 95 per cent of the resident population. For all of this evident over-trapping, however, the spring “sign” appeared to be no more light along the trapped creek than along the one that was not trapped, which at least suggests heavy natural losses on the latter, even after making allowances for spring movement.

Wintering conditions were more benign but still far from optimum on Round Lake in 1936–37 when the water froze to the bottom all over the marsh. The 1936 summer data on breeding adults are of superior accuracy, and, from these and the age ratio from fall and winter specimens, the population entering the winter was computed at about 590 individuals. In late April, 1937, a breeding population figure close to 172 individuals was arrived at. After subtracting from 590 the 181 state-trapped specimens and 12 known to have been speared illegally, 225 remain unaccounted for, including animals that prior to the spring census left the marsh to live elsewhere. Tagging and other data suggest that something less than 100 muskrats moved from Round Lake to neighboring marshlands in March or early April.

Losses through winter-wandering cannot be calculated from the data in hand with definiteness, but they may at times be spectacularly heavy. During the winter of 1926–27, I found around the shores of the Tetonkeha Lakes in eastern South Dakota carcasses of 12 muskrats, most of which had plainly died of cold after wandering about the countryside; and, so far as I know, this was not a winter of unusual emergency for muskrats.

DISCUSSION

The evident severity of the muskrat population declines that may in one way or another be precipitated by drought naturally raises questions as to means and rates of repopulation.

If muskrats have been exterminated over county-wide areas, no noticeable repopulation may take place for years, but it often happens that a nucleus of breeding stock may survive here and there sufficient to permit fairly rapid recovery when habitat conditions again become favorable. Moderately low populations do, in fact, seem to show greater net rates of increase than populations living at high densities, provided that the capacity for accommodation of their habitats is high; for populations studied under these conditions, adults and independent sizes of young seemingly enjoyed greater freedom in choice of habitats with consequently less intraspecific strife and attention from enemies. There is some evidence that the birth of four litters of young per female instead of the usual two or three (Errington, '37c) may be more likely to occur in underpopulated environment, although there is also evidence that mating may not be so efficient at lower densities.

Spring movement into winter-depopulated but currently inviting habitats has been frequently recorded. By the middle of March, 1938, muskrat "sign" was uniformly distributed along a stretch of six miles of Squaw Creek that had been muskrat-vacant most of the winter, and the population elsewhere along the creek had not only been unusually low but had been subjected to more or less trapping. The 1937 breeding population on Little Wall Lake almost certainly moved in from neighboring watercourses during the spring.

SUMMARY

Recent drought seasons have provided exceptional opportunities for the study of muskrat populations living under emergency conditions. Although the animals may show considerable tolerance to habitat changes and may modify their living routines accordingly, their behavior remains basically rather stereotyped.

A large proportion of the muskrats resident in drying out habitats tend to stay in familiar home ranges, and, while they may suffer heavy or even annihilative mortality, they are usually more fortunate than the animals that attempt to go elsewhere. As vicissitudes become intensified, there is a conspicuous increase of intraspecific strife, vulnerability to predation (notably by mink), random and often lethal wandering, and, in winter, losses from hunger and cold.

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IMPROVEMENT OF UNPRODUCTIVE AND ABANDONED PEATLAND FOR WILDLIFE AND RELATED USES

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The peatland of this country has been a subject of public and scientific interest for more than half a century. The acreage of peat and muck claimed by the various states is estimated at 80,000,000 acres.¹ Many areas in sections paralleling the main transportation arteries and within short distance of large centers of population have been reclaimed for the growing of field crops and vegetables including celery, onions, cabbage, lettuce, potatoes, sweet corn, beets, asparagus, mint and others. However, only a small percentage of the total available area is suited or presently required for normal needs of high value crops. Economic conditions and market demands have not justified the cost of reclamation in many cases, and difficulties of various kinds have exercised an increasing adverse influence. This is especially true of certain cultivated areas of peat and muck that are located along stream channels, bordering certain types of lakes and ponds, and those that accumulated on flat plains or valleys underlain by sand or bedrock. Yields of crops have been observed to diminish and many areas have been abandoned either because of long continued shrinkage and subsidence of peat layers, overdrainage, underground fires, accumulation of injurious quantities of salts at and below the surface, crop diseases, and other limiting conditions.² Any development that promises to restore conditions of such areas for native vegetation and wildlife, increase ground water supplies, and prevent excessive damage from drought, fire, or floods should receive consideration. The solution of improvement problems is difficult. It requires time, detailed study, and experimental demonstrations to show clearly the proper relation of effective factors at different seasons, how to restore conditions by adequate methods, and what other changes to anticipate by remedying defects. Although some information on environmental control of peat land has been gained, much further investigation is needed if peatland utilization is ever to be placed on a scientific and sound practical basis.

In dealing with the subject of peatland improvement, a distinction is necessary between areas of peat along river courses, those bordering lakes and

¹ The area of peat and muck is variously estimated to be 79 to 102 million acres (*Senate Document 443, 60th Congress, 1st Session, 1908*).

² The total acreages in drainage enterprises, delinquent in taxes, abandoned, and unimproved in various states are shown in the report of the National Resources Board, 1934, p. 342.

ponds, and those occupying flat or nearly level upland. In origin and formation these three classes of peatland are different. They are the product not alone of different contemporaneous vegetation and environmental conditions, but of diverse past conditions as well, and each is responsive to change through the influence of various factors. This makes possible improvements of peatland in localities where various conditions have changed, but it requires different methods in the actual work of restoring individual types of peatland to natural conditions (fig. 1).

In this presentation no attempt will be made to discuss in detail the methods upon which the following statements are based. Some are now well recognized and generally accepted, particularly the steps which are based on general ecological principles and lead to the natural reestablishment of the original vegetation. It is recognized also that much progress has been made by the U. S. Biological Survey toward a solution of the propagation of plants valuable for wildlife, and the relationships of various species of birds and other animals to native environmental conditions. These and other investigations on changes in plant cover, rate of recovery, wildlife populations and their requirements, have not been considered, as yet, in relation to the three classes of peatland mentioned above. Research along the lines indicated would clarify an understanding of rehabilitating requirements, developmental stages of vegetation, and the plant and animal communities which are effective in changing the appearance of habitats, or have an important temporary or permanent effect upon peat areas that have been inundated. Restoration, improvement, and use of these different types, primarily for wildlife, are in keeping with conservation and land utilization policies. They differ only in the results sought for, that is, in preventing ill-advised and unsuccessful farming operations, in applying restorative measures to meet the needs of different kinds of peatland conditions, and in averting burning, deterioration, and abandonment of a valuable national resource.

An extensive acreage of peatland is found in the southeastern States, in the Great Lakes States, and in the Pacific Coast region. Consolidation of individual tracts may be necessary in some cases before improvement will lead to benefits from protective efforts. But in many states the acreage of peatland is usually made up of small units. Some of these small areas have been incorporated as parts of successful farm units for pasture, hay, and special crops but other areas have not proved to be suited to the usual farm enterprise. At one time they maintained a variety of wildlife. They would again support some kinds of game on the farm if restored and developed for birds that are valuable as insect destroyers, and for fur-bearers. Peatland is economically significant for other than agricultural uses. It can be improved and utilized wisely for the protection of wildlife, the growth of timber, or other practical benefits and, at the same time, conserve surface and ground waters, mitigate floods and subsequent stream erosion, and preserve organic raw material for future generations.

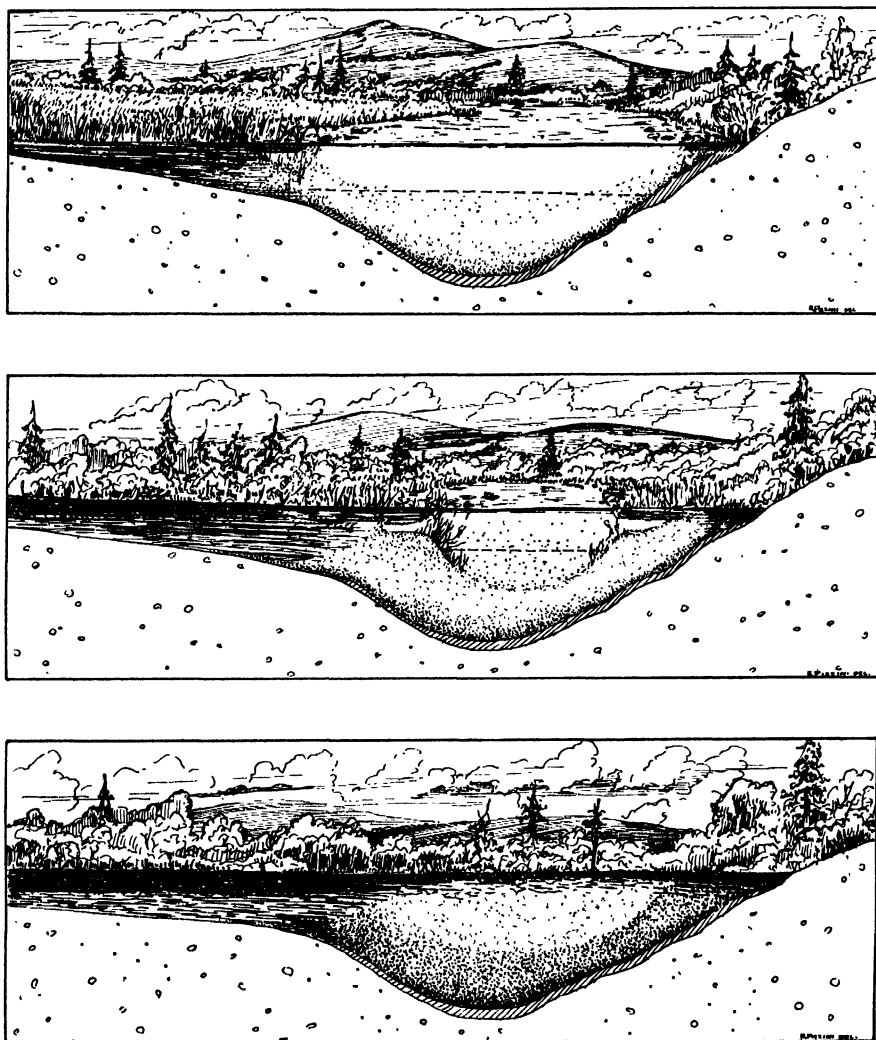


FIG. 1. Diagram illustrating vegetation units, their general succession, and the influence each has in the origin, formation and history of peatland. Three major stages are shown in which peat-forming plant associations displace one another and give rise to a sequence of different layers of peat. They represent aquatic, marsh, and swamp forest vegetation that contribute to the formation of sedimentary, fibrous, and woody peat respectively. The effects of vegetation in developing distinctive profile features and reactions of peatland may begin in open water of lakes, ponds, reservoirs and stream channels, and on flat upland, sandy plains, and even on bedrock. The sketch aids also in recognizing the vital relationship which peat-forming vegetation has in absorbing rainfall, retarding run-off, raising the ground water to higher levels, and storing water supplies. Peat profile studies have significance in classification and mapping, and also in any well considered plan of peat land utilization, for agriculture, industry, water conservation, protection of wildlife, as well as in working out, an effective program for restoring natural conditions on burned-over, deteriorating, and abandoned areas of peat and muck.

IMPROVEMENT OF PEAT AREAS ALONG RIVER COURSES

Non-agricultural and abandoned areas of peatland along streams and coastal river channels offer many opportunities for wildlife and related uses. Striking differences exist between the plant and animal communities that border a stream in flood-plains, and the vegetation and wildlife along a river of which the current is swift and erodes the floor and sides of its channel. On the whole the vegetation supported by eroding streams is sparse and its establishment takes place slowly and irregularly. Free-floating plankton and rooted aquatics utilized by fish and water fowl are usually absent on a bottom of shifting sand and gravel, except in sluggish stretches and more isolated pools where some protection is afforded. The various submerged and rooting species of pondweeds and water plants with aerial foliage are rarely present where silt is deposited. Bays, jutting points, and other variations in shore line are of importance to surface and bottom communities and to pure and mixed stands of vegetation responding to site conditions. In older phases of river activity and in base-leveled streams various plant communities steadily contribute to raising both the bed and the banks of the river until it reaches a condition where the gradient is slight and the rate of flow is very slow. Erosion is not wholly absent but as the stream meanders, the developing vegetation shows a quite definite sequence of stages in a succession. The characteristic communities of the stream bottom include algae, plankton, and a population characterized by rooted aquatics, infusoria, small crustacea, larvae, worms, insects, and others. Organic sediments accumulate over the bottom of a stream at an unknown rate and the composition of flocculent and plastic material varies and needs further study. The stabilized shore line comprises a marginal zone of sedges and marshy grass-like plants forming a more or less floating fringe of fibrous peat that rarely forms organic sediments objectionable to wildlife. A variety of the herbaceous plants endure transplanting and have the ability to recover after a fire and to produce shelter and shade and rootstocks or tubers for feed. In the background is a zone of shrubs and trees developing a layer of woody peat. The woody plants provide both cover and food for many species of wildlife. In composition and value they vary with the character of the swamp forest and the climate of the region. It is only in loop-like channels, abandoned by the river for a more direct route, and which are stagnant and becoming ox-bows or sloughs, that a succession of cattail, reeds, and others may give rise to the periodical necessity of clearing away or at least reducing the growth of peat-forming plants.

At the mouth of rivers that empty into the ocean, the maritime peat areas embrace distinctive salt water, brackish, and fresh water marshes that are of little agricultural value. General experience with the use of drained portions as agricultural land has shown failures that are clearly demonstrated by a continued shrinkage and subsidence of peat layers, the necessity of removing water by pumps, or constructing dikes and levees to prevent access of salt

water in areas at tide level. It should be realized that the value of marshes and sloughs in their primitive condition along coastal rivers and inland streams is the service which they render as homes for fur animals and as feeding grounds for wild ducks, geese, and other migratory waterfowl that are now being seriously reduced in numbers.

Clearing, burning, ditching, removal of streamside brush, straightening of creek and river channels are among the common practices to increase the acreage of crops or pasture on peatland along streams. These practices serve to increase the susceptibility of many rivers to bank erosion. As a consequence flood waters tend to erode banks over a wider frontage and contribute annually to great losses of soil, water, and life of various kinds. The improvement of such peat areas for wild fowl, fur-bearers, and fish is very largely a biological problem. Conditions favorable for the establishment and maintenance of native vegetation on denuded and burned areas of this type of peat land should be reconstructed through minor engineering devices that are inconspicuous as well as inexpensive and which will preserve a natural appearance.

Among the biological problems which will need attention are those of introducing desirable plants and increasing by means of fertilizers, perhaps, if necessary, the reproduction of those already present that may serve as food, provide shelter, or prevent excessive erosion during periods of high flow of water. In order that work of this kind may be based on authentic facts and the methods of environmental control be relied upon to give the best results, it is desirable that a stream and its watershed should first be surveyed. Definite information must be obtained regarding the normal character, distribution, and life forms of dominant plant communities, variations in peat profiles, quality of water, depth and nature of bottom, size and location of pools, riffles, and barriers in the stream, springs, dams, sluggish and eroding currents, and character of polluted water. This type of fieldwork on general stream conditions can be taken up in a more intensive manner under a cooperative agreement with state and federal agencies interested in the protection of watersheds and in stream improvement in different parts of the country.

The possibilities of improvement include a fringe of streambank vegetation reconstructed by means of rushes, sedges and reed-like grasses with freely branching roots and firmly matting rhizomes; shrubs with recumbent branches which root from the tip when they reach water; or by cuttings of poplar and willow planted at points where destructive stream action is developing. Such plants have enough impeding tendency to slow down the current along shore, rebuild the banks, accelerate the spreading of vegetative cover, and force the scouring action of flowing water toward mid-channel. Transplanting and seeding should be tried on peat areas that have been denuded. The rate of recovery will vary greatly, depending upon the character of the original vegetation and on the damage done to the type of surface peat material. Information regarding plant and animal assemblages in large and small rivers is handicapped to some degree by lack of knowledge regarding the life history of

some of the prevalent and conspicuous species, and the effect of fishes and other animals in keeping a stream channel clear from dominant forms of aquatic vegetation.

IMPROVEMENT OF PEATLAND BORDERING LAKES AND PONDS

In lakes and ponds the border of peat-forming vegetation is not merely a mass or haphazard crowding of different plant species. In each water basin there are comparatively narrow zones which represent a certain ecological development. A succession from simple plant communities to intermediate and more highly differentiated plant associations affords a variety of food and shelter for wildlife. Each stage of vegetation contributes plant remains, each builds up a layer of peat superimposed upon one another, and each changes constantly the character of the substratum and ground water conditions, thereby bringing about conditions for a more permanent stage of vegetation and related wildlife.

Beginning in an open body of cool, clear water with a moderate supply of mineral salts from a sandy, clayey, or bare rock bottom, the first stages of plant life include free-floating microscopic plants, submerged rooting aquatics, and pondweeds with aerial or floating leaves, and emerged stems. They offer an effective shelter for young fish and an abundance of natural food for various forms of wildlife. In the course of time the large leaved species shade and crowd out more desirable plants and this stage of vegetation is replaced by cattail, sedges, and reed-like grasses, anchored in the water by freely branching roots and an extensive development of rootstocks. Any attempt to prevent the growth of objectionable plants and secure a balance of conditions becomes one of artificial control. Unless weakened through the loss of leaf surface, the rootstocks build a firm fibrous and buoyant mat over the organic sediments from the aquatic stage. A corresponding change in water level, in volume of peat material over the mineral substratum, and in the quantity and condition of the ground water imposes gradually a stage of woody shrubs and, finally, swamp forest.

There are numerous lakes and ponds of greater or less depth which furnish a good illustration of the early stages of plankton and bottom types of vegetation. There are many others that exhibit strikingly a complete sequence of successions, and still others that have been drained, leaving flats covered with stumps of dead trees and shallow pools of water or irregular patches of black sticky organic sediments and gray marly or diatomaceous residues. The drainage and cultivation of such areas is difficult. There is a long continued shrinkage and subsidence of peat layers, the amount of which varies with the character of the profile and depth to the mineral substratum. In several states the reestablishment of abandoned lake-formed peat areas has been confined to the restoration of former lake levels by blocking outlets and drainage channels, and developing a greater storage of water. • The use of methods for trans-

planting and improving desirable vegetation stages has not been undertaken as yet in places where possibilities of natural reseeding are poor.

The management of unfavorably balanced plant and animal life in lakes and ponds accumulating peat materials is a subject which requires investigation of the various limiting factors as well as methods for controlling them. Standing water develops plankton, bottom communities and other successional stages much more rapidly than running water. Studies should be made on inundated peat areas and bodies of impounded water the age of which is definitely known. This phase of the problem and the measures that would be effective in controlling biotic successional stages are beyond the scope of the present paper. Some of the principal unfavorable environmental conditions, more or less prevalent in such areas, are the following:

(1) Volume and rate of formation of soft, structureless, gelatinous organic sediments which accumulate over the lake bottom from the plant remains of algae and plankton, and from organic suspensions through which the water becomes clouded and light penetration is materially hindered. The development of this material represents perhaps the most serious general condition in lakes and ponds of average depth. The sediments vary in plasticity, content of colloidal material, permeability to air and root development and they shrink greatly on drying, harden, and rarely regain water absorbing capacity. In the smaller and shallower lakes and in the water of quiet bays the dark color of the water is due to a black oozy mass in an advanced degree of anaerobic decomposition. It is frequently buoyed to the surface by gases liberated during the decomposition of the material and may have an injurious effect upon the biological and sanitary conditions of the water. This type of decomposable debris is favorable to the development of a form of "duck sickness" related to botulism and, in part, responsible for the extermination of desirable species of fish and related animal life. Laboratory studies and microscopic examination of suspended and flocculated organic material should be extended to cover observed and hypothetical conditions of sedimentation in basin-formed peat areas.

(2) Overcrowding by relatively less valuable forms of plant life, in particular species of *Chara* precipitating carbonate of lime, and in a lesser degree certain lime-encrusting species of *Potamogeton*. Both tend to form a gray, brittle layer of marl and differ greatly in nutritive qualities. Plant communities of this kind are difficult to control or improve. They compete with pond-snails, crayfish, aquatic insects, as well as duckweeds, arums and others that serve as a food supply or for shelter to fish and other animals. Some experimental evidence on the quality of water in relation to types of plants that are responsible for acid reactions and may affect the composition of lake-and-pond waters would be of considerable value.

(3) Unfavorable physical and chemical changes produced during incomplete decomposition of plant remains from aquatic, marsh, and bog shrub stages of vegetation. The most conspicuous characteristics related to the

water-logged conditions of decay are marsh gas, hydrogen sulphide, a low content of oxygen, and acid reactions. Improvements in the character of conditions may sometimes be made by providing adequate control of water level, and cleaning out springs and indefinite outlet channels. The lack of information based on experience with environmental conditions is partly the reason why less work has been done in the improvement of conditions for wildlife in lakes than of streams.

It is obvious that each lake and pond, supporting peat-forming vegetation, is a problem in itself and that a careful survey of local profile features and environmental conditions is essential. It should precede the selection of areas on which improvement work is contemplated.

In view of the various limiting factors it is evident, also, that the great need in lake and pond improvement is a series of carefully controlled experiments designed to offer possibilities of success in those forms of biological work which restore water, shelter, food, and nesting conditions for wildlife. The studies should not be confined to any one locality, but should be carried on concurrently in several widely separated regions with a diversity of successional vegetation stages and climatic conditions.

IMPROVEMENT OF PEAT AREAS ON UPLAND

There are many important and extensive areas of peatland which did not develop in depressions of flowing or standing water but were built upon relatively flat, level land under conditions of a rising water table. Peat-forming vegetation may establish itself either upon bare rock, as in the case of the Florida Everglades, or on sandy plains, as in the Okefenokee Swamp in Georgia and Dismal Swamp of Virginia. The former was built up by sawgrass marshes and the latter from a succession of two to three different forests dominated by cypress, gum, and tupelo. Noteworthy illustrations of this type of peatland development are in the Great Lakes states where reed and sedge marshes, heath bogs, and spruce and tamarack swamps have been the chief units of vegetation active on a substratum normally deficient in moisture. Practically every unit has a large number of plants of value in providing cover and food for wildlife.

General experience with the reclamation of such areas for agriculture reflects a relative lack of success. Overdrainage has been the cause of many failures involving changes in water level of adjacent mineral soils, and disastrous peat fires have laid bare a discouraging acreage of sand and rock. Small bodies of this type of non-agricultural and abandoned peatland are widely distributed in this country and the total acreage reaches a considerable amount. To achieve the best use of such areas the restoration of former water levels is not only desirable and economically justifiable but also necessary from the viewpoint of a national water policy. Without some control of drains and fluctuating water levels the reestablishment of vegetation native

to these areas takes place slowly and irregularly. If the original plant cover is totally destroyed by plowing, fire, or overdrainage, a rapid evaporation from the exposed surface material may bring about excessive concentrations of soluble salts and thus intensify difficulties. If the area of peat is subsequently abandoned, a variety of annuals and weeds that are hosts to insects injurious to crops may soon form a complete cover. There is a natural tendency for perennials of the original vegetation to reseed the area if the disturbance has not been too great. Weeds cannot compete with native perennials such as sedges, shrubs, and others. Consequently weeds are gradually replaced, usually through intermediate stages. Peat profile sections indicate that, depending upon the character of the original vegetation and the damage done to the peat or muck, the recovery is fairly rapid in rate and relatively complete where some protection is afforded, precipitation is absorbed, and a rise of water level is well under way. It is fallacious to assume that deterioration of submarginal peatland would not continue with practices which lead to exposure of the surface organic material to evaporation, lowered water levels, burning, or salt accumulation. These conditions are difficult to correct by any ordinary method of fertilizing or cropping. Restoration of ground water levels and storage of water supplies are among the primary requirements. They can be brought about by utilizing peat areas for the absorption and infiltration of the normal precipitation, by blocking run-off, constructing small check dams, reducing fluctuations of water level, and reestablishing and maintaining a native vegetation cover adequate for food supplies and shelter for wildlife. The value of these peat areas and their preservation for wildlife possibilities, breeding fur-bearers such as beavers, muskrats, and minks, protecting game and wild fowl should be in most cases of major economic importance. Consideration should be given, also, to impounding water supplies as reservoirs within these areas in order to attract migratory, insectivorous, and other birds. Coordinated with an adequate development of the native swamp forests for timber products, there is much that can be done through the use of unproductive types of peat on upland which have heretofore been neglected. It is hoped that such a program of improving and using peatland resources primarily for the needs of wildlife, may be undertaken without undue delay. An attempt should be made through cooperative agreement to perform this type of research in order to remedy conditions that are economically baneful in many communities.

FUTURE WORK IN PEAT INVESTIGATIONS FOR WILDLIFE.

This brief outline of problems and measures to safeguard different kinds of submarginal peatland and to protect them against agencies of deterioration is intended to be suggestive only. It has been shown that peat investigations can contribute something to an understanding of the fundamental problems of peatland in relation to water conservation and wildlife restoration. Peat investigations can, also, assist in performing research and improvement

work where coordinated restorative measures are to be applied. Briefly restated the more obvious problems for consideration are these:

There are areas of peatland in coastal and continental regions of the United States that are unsuitable for agricultural purposes. They constitute distinct classes of peatland which occur along streams, certain types of lakes, and on flat plains underlain by bedrock or sand. They could be restored and are feasible for rebuilding wildlife refuges as well as for conserving water supplies. The principal task now, and probably for many years to come, is to reestablish natural conditions of marshy lakes, heath bogs, and swamp forests that are over-drained, burned, abandoned, or inherently unproductive for agricultural crops. The character of these different classes of peatland is such that their deterioration will continue unless restorative measures are soon forthcoming. Their withdrawal from agricultural uses is not merely desirable from the point of view of conserving resources of organic material, but is also highly essential to the economic and social welfare of the Nation, and in harmony with the new program of submarginal land retirement and land use to the purposes for which they are best adapted.

Peat investigation can give these problems careful consideration. Its activities in the past, and its accomplishments up to the present do not need to be enumerated; they have been reported elsewhere.³ Ecologically and pedologically sound and practical methods are available that would provide the necessary basic information required to improve different classes of unproductive peatland for the needs of wildlife. A few of the future problems to be solved cooperatively include the following.

1. Examining in detail the differences in surface materials, inherent profile features, and nature and extent of deterioration of peatland in regional divisions and special localities in order to meet the individual needs and possibilities of the areas to be restored;
2. Increasing by suitable methods of propagation a diversity of plants valuable for food and cover on peat areas varying widely in profile features, bottom configuration, character of water supply, and nature of mineral substratum;
3. Reestablishing and improving lakes, ponds, and fresh-water marshes of critical importance in watersheds and headwater streams, and tidal marshes that were once great breeding grounds for migratory and other wildlife;
4. Controlling water levels in relation to type of peat material and character of desirable vegetation, and on which to base reliable studies on the amount, rate of formation, and effects of sedimentary peat;
5. Regulating the main trend of successional stages of vegetation on denuded peatland, areas of peat with impounded water, and peat areas amenable to timber restoration;
6. Determining the essential characteristics of ecological variations in-

³ Dachnowski-Stokes, A. P. Peatland for wildlife. *Amer. Wildlife* 26: 62-63, 1937, illus.

cluding heath bogs, swamp forests, and the conditioning factors of peat materials, water levels, and influences of various other external or accidental factors of their edaphic environment;

7. Providing suitable biological relationships for desirable game, fur-bearing, and other animals, and recording changes and factors of new reactions;

8. Determining and controlling the chief factors underlying the undesirable physical and chemical changes of decomposing plant remains and peat materials that cause diseases to wildlife;

9. Examining and alleviating the effects of drought, saline groundwaters, fire, and other damages;

10. Developing peat areas as feeding and resting places and adequate wintering grounds along the Atlantic, Mississippi, Central, and Pacific migratory routes.

The restoration of peatland located strategically with reference to migratory flyways, and as resting, feeding, and breeding grounds for various forms of wildlife would insure the conservation of peat resources and likewise make an important contribution to economic land utilization not heretofore available. It would provide a series of regional coastal and continental areas where studies and research could be carried on for comparison under varied conditions of climate, vegetation, altitude, topography, water tables, and types of peatland. Much needed information could be obtained from areas of peat-forming vegetation bordering streams and lakes and occupying inundated flat land, their changes during development, and the particular species of wildlife associated under the changing field conditions.

In order to cooperate in this work, and to advise and assist the respective State and Federal agencies in the restoration and management of peatland for wildlife, it is essential that peat investigations be in a position to give adequate, coordinated, and effective aid to these interests in field work, control-plots, and field-scale experiments. Knowledge of peatland, its origin, formation, and interrelationships with wildlife is, of course, basic to restoration and management projects. Peat investigations recognize these relationships and can contribute to the accomplishment of wildlife and related objectives.

STUDIES ON THE ECOLOGY OF SECONDARY COMMUNITIES IN A DECIDUOUS FOREST AREA

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In connection with a study of the community aspects of the activities of birds in an agricultural area in northern Illinois, the writer became impressed with the fact that no satisfactory classification of the community types found in such an area had ever been set forth. Existing systems of ecological classification have been based largely on studies of primitive communities, and are only partially applicable to an area of this kind.

Ecological problems involving secondary communities in which human influence is present as a relatively constant factor have been investigated to some extent by British ecologists (Smith and Crampton, '14; Stapledon and Jenkins, '16; Salisbury, '18; Tansley and Adamson, '26; Godwin, '29; Adamson, '32; Fenton, '34). These studies, however, have been principally botanical, and usually have been carried on in connection with research on pasture problems.

Somewhat similar studies have been made in America in connection with the relation of grazing to forest reproduction (Loveridge, '24; Lutz, '30). A foundation has also been laid for an approach to the theoretical side of the problem presented by man-influenced areas in the work of Shelford ('12, '35), and Clements ('36). In none of these studies, however, has a classification of the secondary communities in such areas been presented in a way to show their relations to one another and to the primitive communities from which they were derived.

The purpose of this paper is two-fold: (1) to present a working basis for the classification of community types existing under agricultural conditions in a formerly forested area; and (2) to consider the relations of the resident avian population of the area to these community types.

The territory studied comprises approximately one square mile. It is situated along the Kankakee River, about a mile from the city of Kankakee, and includes a small portion of the suburban village of Bourbonnais. The part of the area nearest the river contains low sand ridges of glacial origin, and is dissected by a number of deep ravines, which are cut through the drift into the underlying Niagaran limestone. The topography of the remainder is less broken, and merges imperceptibly into the level plain.

The original forest belt along the river at this point was apparently about three-fourths of a mile in width. So far as can be ascertained from present-day remnants, this forest was red oak-sugar maple in the better-watered

localities, and white oak-hickory on the dry sandy hill points. Some trees still remain from the original forest, but most of the timber was cut about 1840, and several small areas of second-growth woods, ranging from 65 to 100 years old, are now present. These are subject to various degrees of grazing and cutting, and also to occasional grass fires, especially in spring.

CLASSIFICATION OF COMMUNITY TYPES

Man-influenced secondary communities of an agricultural area may be divided into two major classes: (1) perennial communities, and (2) subperennial communities. Perennial communities occur in uncultivated areas, including pastures, field borders, permanent meadows, uncultivated orchards and dwelling environs. In such communities the normal succession is usually modified by grazing, cutting, burning or planting. Subperennial communities occur in areas where cultivation prevents the development of any except transient assemblages of plants and animals. The perennial communities of pastures, field borders, meadows and orchards may be thought of as constituting the ecological groundwork of the region. They border upon and enclose the smaller communities of the dwelling environs and the subperennial communities of cultivated fields.

The centering of human activity in and about the communities of the dwelling environs brings about the creation of a particular assemblage of plants and animals, in which some wild forms find a place, and in which a great many introduced species (both plants and animals) normally occur. These communities, usually of relatively small extent in rural areas, and the subperennial communities of cultivated fields, may be thought of as constituting "islands" of special conditions within the ecological framework. Such "island" communities may be designated as "edificarian insulae" in the case of the dwelling environs, and "subperennial insulae" in the case of the cultivated fields.¹

In the area included in this study orchards are entirely absent, and meadows are of relatively small extent. Therefore pastures and field borders make up nearly all of the perennial communities outside of the edificarian insulae. The plant and animal components of these communities are derived chiefly from the original forest edge. The more open community types, however, contain some species which were originally typical of the prairie, while the more brushy types contain some forest species from the original oak-hickory and oak-maple associations.

The extent to which forest edge conditions are approached in the communities of pastures and field borders is dependent on the degree of human influence exercised through grazing, cutting and burning. The different com-

¹ This essentially insular nature of cultivated fields holds true even in cases where the cultivated areas of a locality far exceed the perennial communities in extent, due to the fact that the field borders which surround the cultivated areas form a part of the perennial groundwork.

munity types, therefore, form a natural series from pure grassland without woody plants, to brushland which resembles true forest edge as regards its plant and animal components, even though it is detached from the forest. The basis for this series is the amount and character of tree and shrub reproduction, and the presence or absence of adult trees. It may be arranged as follows:²

- I. Communities without shrubs (open communities)
 - a. Without trees (open grassland)
 - b. With trees (open woodland)
- II. Communities with shrubs (shrub communities)
 - a. Without trees (shrubby grassland)
 - b. With trees (shrubby woodland)
- III. Communities with shrubs and tree reproduction (detached forest edge communities)
 - a. Without trees (early detached forest edge)
 - b. With trees (old detached forest edge)

These community types represent stages in deflected successions (Godwin, '29) leading to proclimaxes (Clements, '36), in which vegetation, wild life and human influence will have entered into a state of dynamic equilibrium. Proclimax conditions probably have not been attained in any of the pastures considered in the present study, but they are reached or closely approached in some of the older field borders.

The accompanying map (Fig. 1) shows the spacial relations of the community types of the pasture-field border series, and those of the edificarian and subperennial insulae. The approximate percentages of the area occupied by these types are as follows: Edificarian insulae (2%), Subperennial insulae (45%), Pasture-field border series: Type Ia (15%), Type Ib (6%), Type IIa (11%), Type IIb (13%), Type IIIa (4%), Type IIIb (4%).

In the pastures the climax trees (*Quercus rubra*, *Q. alba*, *Acer saccharum* and *Carya* sp.) usually survive only as adults. Normal reproduction of them is going on only in the protected relict fragment communities, such as those occurring along ravines. The woody plants which are now reproducing in pastures are usually those which possess some sort of protective adaptation to enable them to resist the action of grazing animals. Such grazing-resistant plants within the area studied include: (1) those which possess thorns or their equivalent in the form of sharp, woody projections at the dead ends of browsed shoots: hawthorn, *Crataegus* spp.; honey locust, *Gleditsia triacanthos*; osage orange, *Maclura pomifera* (introduced); crab apple, *Pyrus coronaria*; wild rose, *Rosa* spp.; (2) those which possess a disagreeable taste or odor: Kentucky coffee-tree, *Gymnocladus dioica*; red cedar, *Juniperus virginiana*;

² This series may be used for the classification of all types of perennial communities except edificarian insulae. Permanent meadows would be classified under Type Ia, and uncultivated orchards under Type Ib.

and (3) those whose rapid growth in spring places the ends of their shoots above the reach of grazing animals by mid-summer when the grass supply begins to fail: willow, *Salix* sp.

As pasture conditions approach proclimax, the climax trees and shrubs tend to be eliminated in all except the protected relict fragment communities

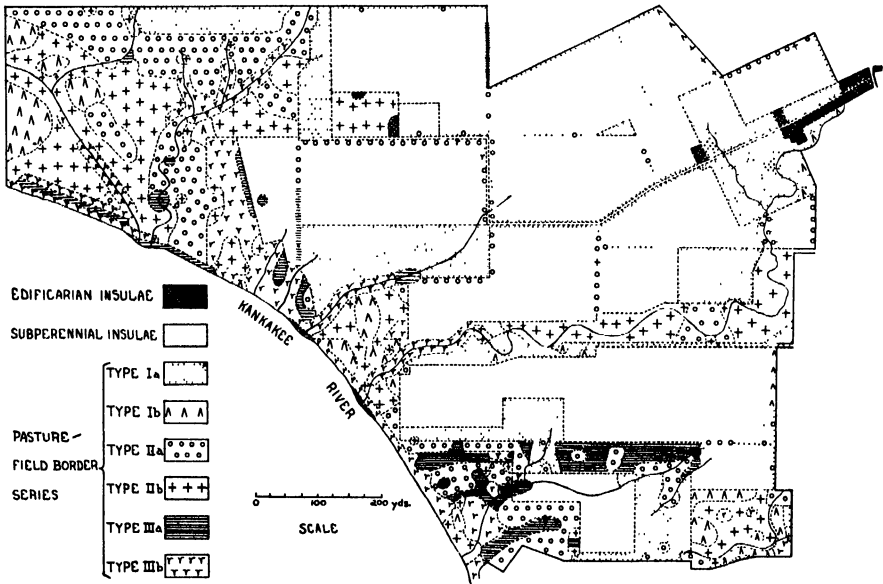


FIG. 1. Map of the Bourbonnais-Kankakee River area, showing the distribution and extent of the community types of the pasture-field border series, and the edificarian and subperennial insulae.

where their reproduction can take place unmolested. Their place is taken by trees and shrubs of the grazing-resistant type. The kind of proclimax eventually attained with the continuation of constant conditions in any particular case will be determined by the degree and kind of human influence, and will be represented by some community type within the series from open grassland to detached forest edge. Except in the relatively small number of cases where trees and shrubs are planted to replace those which die or are destroyed, this proclimax will probably tend to be one of three types: (1) open grassland (Ia); (2) shrubby grassland (IIa); or (3) old detached forest edge (IIIb). The accompanying diagram (Fig. 2) shows the probable relation of the present community types to these proclimaxes.

This gradual change in the direction of a proclimax condition is going on at present in the pastures studied. Evidence of it is found in the lack of reproduction among climax trees, and the progressive elimination of these trees, together with the occurrence of all stages of reproduction among grazing-resistant trees and shrubs.

The community types found in partially protected locations within the pastures, as along stream banks, on rocky slopes, and in ravines, generally tend to more nearly approach forest edge conditions than do those found in the adjacent unprotected localities. In unlevel areas the degree of develop-

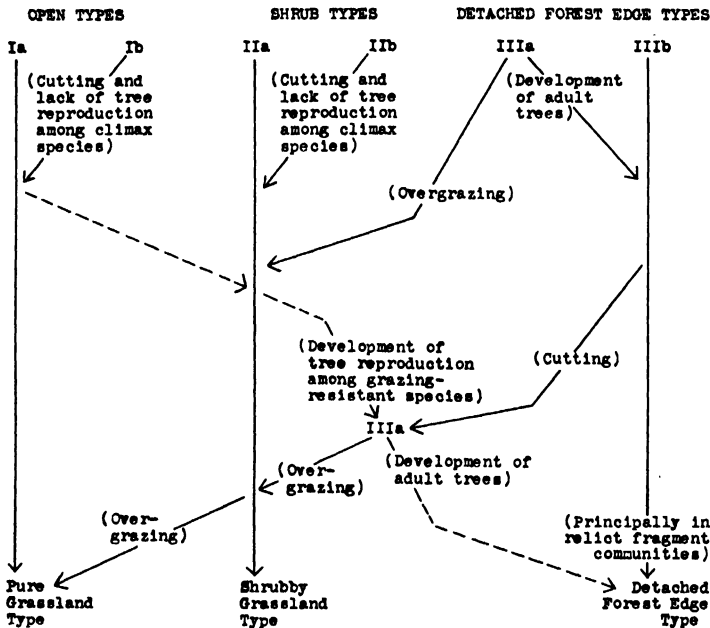


FIG. 2. The probable course of development of proclimax types in pastures under constant human influences, exclusive of planting. The solid lines represent the more probable trends, and the broken lines the less probable trends.

ment of forest edge conditions is usually proportional to the amount of protection afforded by the topography. This tendency culminates in the true relict fragment communities, containing all reproduction stages of climax trees and shrubs, and many species of herbs and small animals characteristic of the forest floor. Such communities are found in the deep rocky ravines, where the nature of the topography completely shuts out the influence of grazing and burning, and very greatly reduces the probability of cutting.

While the community types of field borders correspond to those of pastures, and are essentially equivalent to them from the standpoint of bird habitability, the fact that grazing is usually excluded and human control is exercised through cutting or burning results in deflected successions of a different type.

The approximate age of field borders may be ascertained by a study of old maps, considered in connection with the age of recently cut stumps, and the extent to which the sodded or brushy field border has come to form a ridge as a result of the plowing and erosion of the adjacent cultivated land.

Evidence from these sources indicates that some of the field borders in the area studied have been maintained in their present location for periods of 65 to 100 years.

The woody plants reproducing in field borders are usually those which develop sprouts tenaciously after cutting. Some of these (hawthorn, Osage orange, crab apple), are also included in the list of grazing-resistant plants. Other important species belonging to this group are: wild cherry, *Prunus* sp.; hackberry, *Celtis occidentalis*; elm, *Ulmus americana*; box elder, *Acer negundo* (probably introduced); wild grape, *Vitis* sp.; poison ivy, *Rhus toxicodendron*; sumac, *Rhus glabra*; elderberry, *Sambucus canadensis*.

If field borders are cut or burned over annually the community type is usually pure grassland (Type Ia); and if they remain unmolested for long periods detached forest edge conditions (Type IIb) will develop. If, however, human control in the form of cutting is applied at irregular intervals of more than one year (as is usually done) the normal succession will be deflected at a shrub stage (Type IIa) or at an early forest edge stage (Type IIIa), and a denuded interval (approximating Type Ia) will occur preceding the sprouting of new growth. When periodic cropping to a uniform level takes the place of periodic denudation, as in the case of osage orange hedges, a cropped shrub interval takes the places of the denuded interval. In any of these cases the community may be shifted to the corresponding "b" type by the presence of trees which escape cutting.

Thus in old field borders a relatively stable proclimax condition may develop at either end of the series (Ia or IIb), or the application of human control at intervals may cause an irregularly cyclic shifting of conditions centering around the shrub and early forest edge stages in the middle of the series. The probable courses and interrelations of these varying deflected successions are shown in Fig. 3.

In all but the most brushy community types of both pastures and field borders the most prominent herbaceous species is Kentucky bluegrass, *Poa pratensis*. Most of the other herbaceous species are either derived from the original forest edge community or are introduced species that have followed civilization. In wooded areas (the "b" community types) a considerable number of forest floor plants still persist, although these are gradually losing ground, except in the protected relict fragment communities.

Two community types occur in edificarian insulae. These are determined, as are the types of the pasture-field border series, by the presence or absence of trees, and may be designated in a similar manner. The "a" type (without trees) is characteristic of the centers of urban areas, and may occur as a temporary stage in rural areas when a new dwelling is established on a formerly treeless location. The "b" type (with trees) is characteristic of the dwelling environs in most residential, suburban, village and rural areas. It usually approximates to a certain extent the shrubby woodland type (IIb) of the pasture-field border series, with the addition of buildings, and the

partial replacement of native shrubs and herbaceous species with cultivated forms and miscellaneous weeds. In old-established rural dwelling environs this community type is relatively stable so long as human occupancy continues.

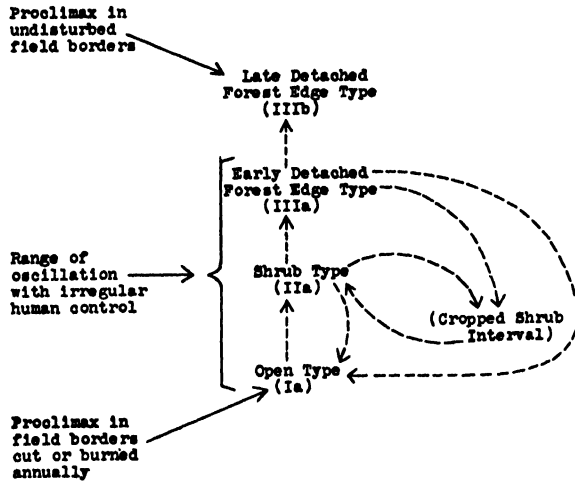


FIG. 3. The probable course of deflected successions and development of proclimaxes in field borders under varying degrees of human control in the form of cuttings.

• Subperennial insulae provide conditions so unstable that the development of any permanent community is impossible, although certain species may persist from season to season. The subperennial insulae included in the present study were planted to corn, wheat, oats or soy beans. In some cases the land was plowed in the fall and allowed to lie barren over the winter. In other cases the stubble or corn stalks were allowed to stand over the winter and the ground was plowed the following spring.

BIRDS AND MAN AS JOINT OCCUPANTS OF A SETTLED AREA

Man-created and controlled conditions are suitable not only for man and his domestic animals, but also for a set of wild animal species including representatives of all land-dwelling groups: invertebrates, amphibians, reptiles, birds and mammals. These animals are those whose habitats have been preserved to an extent sufficient to permit of their survival, or whose range of physiological tolerance is sufficiently great to enable them to adapt themselves to the new habitats which man has created. In a sense each species or group represents a special case in which the particular conditions which permit of its survival have been preserved or created, such preservation or creation in most cases having been merely incidental to the carrying on of human activity.

Since man-tolerant forms have survived for essentially different reasons in the case of each species or group, and since in the aggregate they represent

only the scattered remains of a primitive fauna with some exotic elements added, they do not in any sense constitute a natural unit or an integrated community. Therefore it seems best to consider them simply as joint occupants with man of the community types which he has created for himself and his domestic animals.

Some of the small land birds are among the most successful of the man-tolerant animal groups. Their joint occupancy extends to all man-created community types. This is partly due to the fact that their great mobility makes it possible for them to take advantage very readily of new favorable situations, and of the increased supplies of food which become available as a result of man's activities. Also in the case of forest and forest edge species, this successfulness is due in part to a lesser dependence on ground conditions (Shelford, '12).

The present study is limited to a consideration of the community relations and activity of resident land birds, exclusive of gallinaceous and raptorial species. Investigations were carried on during the winter and summer seasons of 1936 and 1937. No special studies were made of bird activity during the migration seasons of spring and fall, though general observations of resident species were continued. The method of investigation was similar to that followed in an earlier study of bird activity in western New York (Van Deventer, '36). Field observations were taken at regular intervals, each observational trip covering approximately 160 acres (one-fourth square mile). Particular attention was given to the number of birds of each species which were present, and to the community type or types in which activity was being carried on by each individual or group. The different species found in association in mixed flocks in winter were also noted.

In general, birds as a group are more abundant in the detached forest edge community types of the pasture-field border series and in edificarian insulae, than they are in shrub types and open types of the series and in subperennial insulae. This is true of both winter and summer residents. The relative favorability of different community types for bird life may be ascertained approximately by comparing the density of the bird population within them, expressed in terms of the number of birds per square mile of each type of habitat. In the following table (Table I) the density of the bird population is shown for edificarian and subperennial insulae, and for the open types, shrub types and detached forest edge types of the pasture-field border series.

TABLE I. *Comparative densities of the winter and summer resident bird population expressed in terms of the number of birds per square mile of each type of habitat*

	Edificarian Insulae	Sub- perennial Insulae	Open Com- munity Types	Shrub Com- munity Types	Detached Forest Edge Community Types
Winter Residents	814	17	42	75	471
Summer Residents	1346	25	131	225	717

It will be seen from this table that the edificarian insulae, while occupying only a small portion of the area (2 per cent), constitute a bird habitat which is superior even to the detached forest edge from the standpoint of bird density. However almost the entire winter bird population, and approximately three-fifths of the summer population found in this habitat consist of introduced species which are semi-communal in habit and therefore tend to thrive under conditions of crowding.

The density of the bird population in the subperennial insulae is decidedly less than in any of the other types. It consists of a small resident group, augmented by individuals and flocks which visit the locality to feed.

The relative favorability of the community types of pasture-field border series, as indicated by the density of the bird population, bears a direct relation to the amount of tree and shrub growth present in them. The least favorable are the open types where human interference is greatest, while the most favorable are the detached forest edge types where this interference is least. The shrub types lie between these two extremes in relative favorability. Since introduced species occupy only a minor place in the bird life of these community types, this gradation represents the response of the native avifauna to a progressive variation in the amount of human influence, as reflected in the extent of development of woody vegetation.

COMMUNITY RELATIONS OF WINTER RESIDENT SPECIES

The area included in the present study supported a winter bird population of approximately 243 per square mile in 1936, and 282 per square mile in 1937. These figures represent estimates based on direct counts taken in connection with the regular observational trips.

The winter bird population is separable into three fairly well-defined sections: (1) Those centering their activity in the edificarian insulae; (2) those centering their activity in the subperennial insulae; and (3) those inhabiting the community types of the pasture-field border series. The accompanying diagram (Fig. 4) shows the distribution of the observed activity of each species in the different community types in winter. In constructing this diagram the observation of an individual in any community type was considered as one unit of activity, and the observation of a flock was counted as a number of units equal to the number of individuals it contained.

The predominant species in the edificarian insulae in winter are the English sparrow and the starling. Both are introduced species and permanent residents. Other species which occur are the downy woodpecker and the slate-colored junco. These appear in the community of the dwelling environs only occasionally and in small numbers during the winter, being mostly transients from the communities of the pasture-field border series. Juncos and other forest edge birds, however, visit the edificarian insulae in considerable numbers during the migration seasons of spring and fall.

In the present study English sparrows and starlings were found together

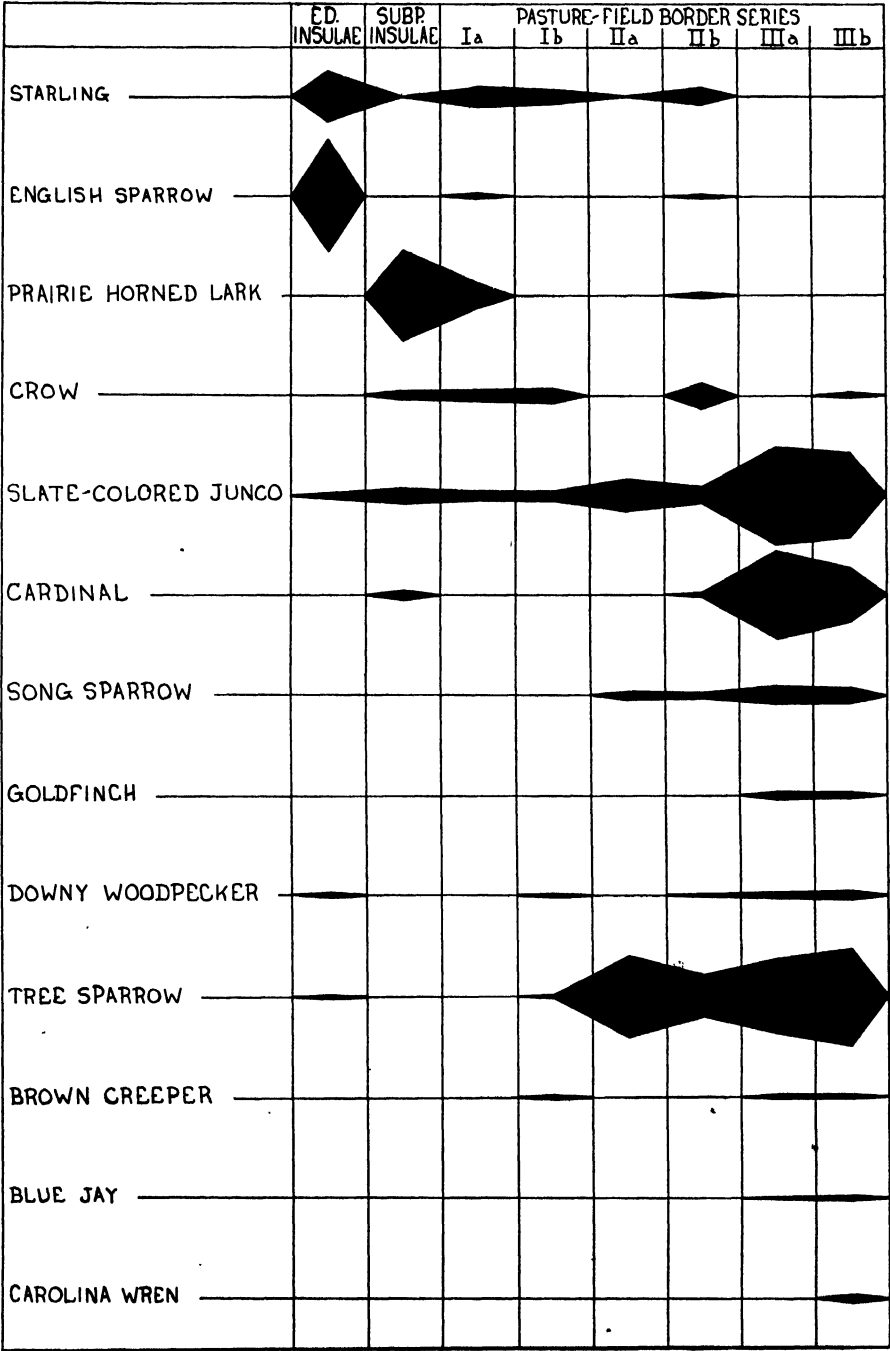


FIG. 4. Distribution of the observed activity of winter birds in relation to community types

in the same habitat in 17.8 per cent of the cases of observation involving either species. Usually, however, the relations of the two species when they were in close proximity were of such nature as to indicate that the association was the result of chance contiguity, and did not represent the formation of a true mixed flock. Each species retained its identity, and the period of association was usually of short duration.

The prairie horned lark is the predominant winter bird species in sub-perennial insulae. This species is the only permanent resident bird found in cultivated fields. Other birds occurring in this habitat in winter are transients from the edificarian insulae, or from the pasture-field border communities. The English sparrow and the starling were found in fields near the dwelling environs, and the slate-colored junco, the tree sparrow, and the cardinal appeared in fields adjacent to the more brushy community types. The crow, while having its center of activity in the community types with trees, ranged extensively over the subperennial insulae. The subperennial communities may be of considerable importance in the winter economy of these species. If weed growth has been allowed to develop following the removal of the crop or the cessation of cultivation, the seeds may furnish an important source of food for birds having their activity centers in adjacent perennial habitats. Waste grain, especially in the case of corn fields, also furnishes a source of food. Forbes and Gross ('23) found the Lapland longspur to be the most abundant bird per square mile in northern Illinois in winter, and to be predominant in all open situations. This bird, however, was not observed at all during the present study.

Prairie horned larks made up 66 per cent of the birds observed in sub-perennial communities in winter, while all of the transient species, taken together, made up the remaining 34 per cent. Association between prairie horned larks and the transient species was noted in only a single case, that being with tree sparrows in a corn stalk field. This almost complete absence of interspecific relation was probably due to the fact that the prairie horned larks occurred mostly in open plowed fields which were not usually visited by any transients except the crow. They did not frequent the vicinity of brushy field borders, nor the localities near the edificarian insulae where other transient species were usually found.

The following species are permanent residents in the community types of the pasture-field border series: Crow, *Corvus brachyrhynchos brachyrhynchos* Brehm., Cardinal, *Richmondia cardinalis cardinalis* (L.), Blue jay, *Cyanocitta cristata cristata* (L.), Song sparrow, *Melospiza melodia melodia* (Wilson), Carolina wren, *Thryothorus ludovicianus ludovicianus* (Latham), Gold finch, *Spinus tristis tristis* (L.), Downy woodpecker, *Dryobates pubescens medianus* (Swainson).

None of these species, however, are present in very large numbers, and all are subject to wide variations in abundance in winter from year to year. In 1936 there were 8 cardinals estimated per square mile, while in 1937 the

number was increased to 16. On the other hand there were 8 song sparrows per square mile in 1936, and only one in 1937; and there were 4 downy woodpeckers per square mile in 1936, and only 2 in 1937.

The tree sparrow, *Spizella arborea arborea* (Wilson), the slate-colored junco, *Junco hyemalis hyemalis* (L.), and the brown creeper, *Certhia familiaris americana* Bonaparte, are winter residents only. Of these the brown creeper is present in very small numbers. During both of the winters included in the present study there was only one brown creeper per square mile. The tree sparrow and the slate-colored junco, however, are the numerically predominant species in all of the brushy community types of the pasture-field border series. Together they constitute the nucleus of a group of small birds which have similar habitat relations in winter, and frequently associate in true mixed flocks.

The formation of such mixed flocks among certain species of small winter birds has been frequently noted (Eaton, '14; Butts, '27; and Chapman, '34). This phenomenon was analyzed by the writer (Van Deventer, '36) for a habitat group of winter birds in western New York, including the black-capped chickadee, tree sparrow, white-breasted nuthatch and downy woodpecker. In this group two or more of the species were found associated in 31 per cent of the observed cases.

In the present study during the winter of 1936 the tree sparrow, slate-colored junco, downy woodpecker and song sparrow apparently constituted a similar habitat group. Two or more of these species were found associated in 33 per cent of the cases of observation for the group. During the winter of 1937, however, when the downy woodpecker and the song sparrow were present in very small numbers, their place in the group was partially filled by the cardinal, which was twice as abundant as it had been during the previous winter. Two or more members of the 1937 habitat group were found associated in 20 per cent of the observed cases.

In general, members of the habitat group during both winters centered their activity in the more brushy types of the pasture-field border series. The slate-colored junco, cardinal, downy woodpecker and song sparrow showed a definite preference for the detached forest edge types (IIIa and IIIb), with the song sparrow showing a further preference for the wet phases of these types. The tree sparrow, however, was slightly more wide-ranging. It showed a primary preference for IIIb, but exhibited strong secondary preferences for both IIIa and IIa (shrubby grassland). These results correspond in a general way to those obtained for the New York habitat group, which was found to have a primary center of activity in the brushy swamp edge, and a secondary center in the upland forest edge, both of which would be included under Types IIIa and IIIb.

Other species of small birds present in small numbers and not directly connected with the habitat group (blue jay, Carolina wren, goldfinch and brown creeper) all centered their activity in the detached forest edge types.

Birds of these species were sometimes found associated with members of the habitat group, but not in a sufficiently large number of cases to warrant their inclusion in it.

The crow showed no connection with members of the habitat group. It ranged widely over all community types except edificarian insulae, but centered its activity in those having trees. It reached its greatest abundance in winter in the open woodland and shrubby woodland (Ib and IIb). No definite crow roosts were located in the area. Therefore the winter crow observations represented activities in feeding and temporary resting places.

Transients in communities of the pasture-field border series consisted principally of English sparrows and starlings, which usually were observed in the vicinity of edificarian insulae, and prairie horned larks, which appeared to some extent in open grassland (Ia). These birds showed no significant interspecific relations with true pasture-field border species.

COMMUNITY RELATIONS OF SUMMER RESIDENT BIRDS

Estimates of the density of the bird population within the area in summer were based in part on direct counts, and in part on the observed numbers of active and singing males of the species that were nesting, each male being considered to represent one pair. By these methods 504 birds were estimated to be resident in the square mile in the summer of 1936, and 576 in 1937.

The bird population in general is more numerous in all habitats in summer than in winter. The summer residents which arrive in spring outnumber the winter residents which leave, resulting in a net increase. The increase is most conspicuous in the open and shrub community types (Table I). This is correlated with the fact that while these habitats frequently offer little in the way of food or protection in winter, they afford a good supply of food in summer and provide nesting sites for some species which select less protected situations.

The interspecific associations which form a conspicuous feature of the winter bird life are almost completely absent in summer. With the beginning of the breeding season the feeding territory of the flock is exchanged for the breeding territory of the pair (Howard, '20), and although the breeding territories of pairs belonging to different species undoubtedly overlap, any association which occurs is apparently accidental. On account of the abandonment of the flocking habit at the beginning of the breeding season in most species, summer field records usually involve solitary birds or pairs, while in winter most records are those of flocks, except in the case of species present in very small numbers. With the close of the breeding season flock records begin to appear again.

The larger summer bird population involves an increase in the number of species as well as in the number of individuals. The following species of birds were resident in the area in summer during one or both years of the present study (p.r. indicates permanent resident; s.r., summer resident):

Starling, *Sturnus vulgaris vulgaris* L., p.r., English sparrow, *Passer domesticus domesticus* (L.), p.r., Prairie horned lark, *Otocoris alpestris praticola* Henshaw, p.r., Cardinal, *Richmondia cardinalis cardinalis* (L.), p.r., Song sparrow, *Melospiza melodia melodia* (Wilson), p.r., Goldfinch, *Spinus tristis tristis* (L.), p.r., Crow, *Corvus brachyrhynchos brachyrhynchos* Brehm., p.r., Carolina wren, *Thyrothorus ludovicianus ludovicianus* (Latham), p.r., Downy woodpecker, *Dryobates pubescens medianus* (Swainson), p.r., Blue jay, *Cyanocitta cristata cristata* (L.), p.r., Brown thrasher, *Toxostoma rufum* (L.), s.r., Meadow lark, *Sturnella magna magna* (L.), s.r., Killdeer, *Oxyechus vociferus vociferus* (L.), s.r., Dickcissel, *Spiza americana* (Gmelin), s.r., Field sparrow, *Spizella pusilla pusilla* (Wilson), s.r., Yellow-billed cuckoo, *Coccyzus americanus americanus* (L.), s.r., Indigo bunting, *Passerina cyanea* (L.), s.r., Robin, *Turdus migratorius migratorius* L., s.r., Mourning dove, *Zenaidura macroura carolinensis* (L.), s.r., Catbird, *Molothrus ater ater* (Boddeart), s.r., Flicker, *Colaptes auratus luteus* Bangs., s.r., Kingbird, *Tyrannus tyrannus* (L.), s.r., Wood pewee, *Myiochanes virens* (L.), s.r., Bronzed grackle, *Quiscalus quiscula aeneus* Ridgway, s.r., Bobolink, *Dolichonyx oryzivorus* (L.), s.r., Red-headed woodpecker, *Melanerpes erythrocephalus* (L.), s.r., House wren, *Troglodytes aëdon aëdon* Vieillot, s.r., Chimney swift, *Chaetura pelagica* (L.), s.r., Rough-winged swallow,³ *Stelgidopteryx ruficollis serripennis* (Aud.), s.r., Bluebird,³ *Sialis sialis sialis* (L.), s.r.

Because of the increase in the total number of birds and in the number of species which prefer the less protected community types, there is a better distribution of bird population over the entire area in summer than in winter. For these same reasons, together with the abandonment of flocking and the establishment of nesting territories, there is also a more individualized selection in summer of certain community types as centers of activity by particular species. Therefore the different types are better indicated by differences in the relative abundance of particular species in summer than in winter. Figure 5 shows the distribution in the different community types of the observed activity of all species present in summer in numbers of 5 or more per square mile.

On the basis of differential distribution of observed activity as indicated by this diagram the following species apparently may be considered as "partial indicators" or particular community types in summer: Edificarian insulae—English sparrow, starling, house wren. Subperennial insulae—Prairie horned lark, killdeer. Pasture-field border series—Type Ia: Dickcissel, cowbird. Type Ib: Robin. Type IIa: Field sparrow. Type IIb: Wood pewee, flicker. Type IIIa: Catbird, brown thrasher. Type IIIb: Indigo bunting, yellow-billed cuckoo.

It is also evident, however, from figure 5 that the three sections into which the bird population of the area was divided in winter, characteristic of the edificarian insulae, the subperennial insulae, and the pasture-field border.

³ Observed in 1937 only.

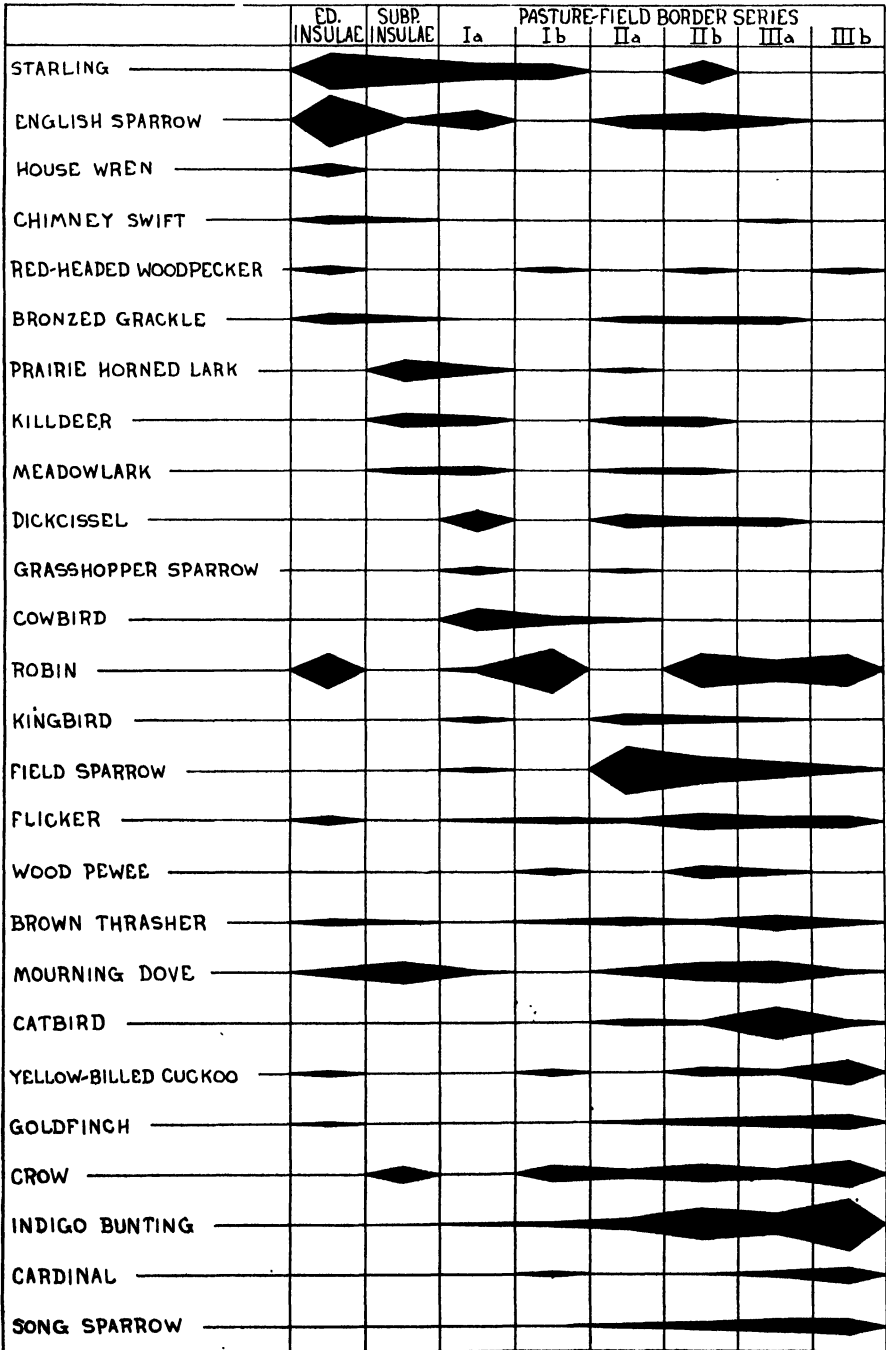


FIG. 5. Distribution of the observed activity of summer birds in relation to community types

communities, are much less rigidly defined in summer. Certain summer-resident pasture-field border birds occur regularly in the edificarian insulae, having wholly or partially adapted themselves to the new conditions existing around human dwellings, including the presence of aggressive introduced species. In the present study the robin and house wren were prominent in the edificarian insular communities, and the goldfinch, brown thrasher, yellow-billed cuckoo, mourning dove, flicker, chimney swift, red-headed woodpecker and bronzed grackle were present in smaller numbers. Four of these species: the house wren, chimney swift, red-headed woodpecker and bronzed grackle, utilized this habitat as a primary center of activity.

Many birds from the edificarian insulae and the pasture-field border communities visit the subperennial insulae in summer, attracted by the food supply. The insectivorous species are attracted by the exposure of the ground-dwelling invertebrate life in connection with cultivating operations; and the seed-eating species by harvested crops, waste grain, and weed seeds. The most frequent visitor noted in the present study was the mourning dove. This species was recorded as frequently in subperennial insulae as it was in its principal nesting habitat (Type IIIa). Other visitors included the starling, English sparrow, crow, meadow lark, and brown thrasher.

Cases in which species from edificarian and subperennial insulae appear as transients in pasture-field border communities in summer are not frequent, and probably represent accidental occurrences. Examples of such chance visitations in the present study were the presence of killdeer in an open pasture adjoining their usual habitat in a cultivated field, and the presence of English sparrows in field borders near the edificarian insulae.

In general the different species tend to be most abundant and active in those community types which most closely resemble the conditions of the original community to which they belonged. Thus the species which center their activity in the community types of the pasture-field border series, with the exception of open grassland (Ia), belong to the original forest edge or forest communities, while those which are predominant in Type Ia and in subperennial insulae were mostly members of the original prairie community. Similarly the introduced species which predominate in the edificarian insulae are also characteristic of man's dwelling environs in Europe. Notable exceptions are found in the case of the forest and forest edge species which have developed the habit of feeding in subperennial insulae under agricultural conditions, or have invaded the edificarian insular communities extensively as residents.

Table II shows the original habitats of the more important native summer resident species, with their present primary centers of activity, and their secondary centers in cases where these were well-marked.⁴

⁴ The original habitats used in this table are taken from Shelford, V. E., 1912. "Animal Communities in Temperate America," and "Naturalists Guide to the Americas," 1926 (Shelford, V. E., editor).

TABLE II. *Original habitats of summer resident birds compared to present centers of activity*

Species	Original Habitat	Primary Center	Secondary Center
Prairie horned lark	Prairie	Subp. Insulae	—
Meadow lark	Prairie	Type Ia	—
Dickcissel	Prairie	Type Ia	Type IIa
Grasshopper sparrow	Prairie	Type Ia	—
Killdeer	Prairie	Subp. Insulae	—
Cowbird	F. E. and Prairie	Type Ia	—
Song sparrow	Forest Edge	Type IIIb (wet)	Type IIIa (wet)
Goldfinch	Forest Edge	Type IIIb	Type IIIa
Brown Thrasher	Forest Edge	Type IIIa	—
Field sparrow	Forest Edge	Type IIa	Type IIb
Indigo bunting	Forest Edge	Type IIIb	Type IIb
Mourning dove	Forest Edge	Type IIIa	Subp. Insulae
Catbird	Forest Edge	Type IIIa	—
Kingbird	Forest Edge	Type IIa	—
Flicker	Forest and F. E.	Type IIb	—
Bronzed grackle	Forest and F. E.	Ed. Insulae	—
Cardinal	Forest	Type IIIb	—
Crow	Forest	Type IIIb	Subp. Insulae
Yellow-billed cuckoo	Forest	Type IIIb	—
Robin	Forest	Type Ib	Ed. Insulae
Wood pewee	Forest	Type IIb	Type Ib
Red-headed woodpecker	Forest	Ed. Insulae	—
Chimney swift	Forest	Ed. Insulae	—
House Wren	Forest	Ed. Insulae	—

A certain amount of adaptation to new conditions is necessary on the part of all native species which have succeeded in maintaining a joint occupancy with civilized man, even though the new habitats which are occupied are those most similar to the original ones. The range of adaptability and the extent of habitat adjustment, however, are greater in the case of some species than others. Those which occur regularly in the edificarian insulae exhibit the most notable adjustment, since this community type had no close parallel before the coming of civilization. They also represent the greatest degree of tolerance to human influence and activity. These species, together with the ones characteristic of subperennial insulae, and of the open and shrubby grassland types of the pasture-field border series (Ia and IIa), are the least likely to be affected adversely by progressive changes in the direction of proclimax, or by any future intensification of human influence in the area.

CONCLUSION AND SUMMARY

Secondary communities in a formerly forested agricultural area may be classified on the basis of permanency as (1) perennial communities, occupying uncultivated areas, and (2) subperennial communities, comprising cultivated areas. Perennial communities of pastures and field borders constitute the permanent ecological groundwork of the area, and they border upon and enclose the essentially insular communities of cultivated fields and dwelling environs. These may be designated as subperennial insulae and edificarian insulae, respectively.

The pasture-field border communities constitute a series ranging from pure grassland to detached forest edge. The community type in each case depends on the amount of human influence exercised through grazing, cutting, burning or planting. In pastures the trees and shrubs which are adapted to resist grazing and browsing tend to survive, while climax forms tend to be eliminated. In field borders species which sprout readily after cutting possess a similar advantage. If relatively constant conditions are maintained over a sufficiently long period proclimax communities will develop.

Animals which survive in an agricultural area do not constitute a well-defined ecological group, but rather represent the remnants of integrated primitive communities which have survived because of special circumstances in each case. Therefore it seems best to consider them simply as joint occupants of the area, along with man and his domestic animals. Their joint occupancy extends to all man-controlled habitats, but they are more abundant in the detached forest edge types of the pasture-field border series and in edificarian insulae than in the open and shrub types of the series and in subperennial insulae.

The total density of birds in the area in winter was estimated to be 243 per square mile in 1936, and 282 per square mile in 1937. The winter bird population may be divided into three sections, centering their activity in the edificarian insulae, the subperennial insulae, and the communities of the pasture-field border series. In the pasture-field border communities the tree sparrow and the slate-colored junco constitute the nucleus of a group of small birds which have similar habitat relations in winter and associate together very readily in mixed flocks.

The bird population in summer was estimated to be 504 per square mile in 1936, and 576 per square mile in 1937. The summer population represents an increase over the winter population in the number of species as well as in the number of individuals. The increase is most conspicuous in the open and shrub types of the pasture-field border series. The population is more generally distributed over the entire area in summer, and there is a more definite selection of certain community types as centers of activity by particular species.

The present bird fauna is derived from the original forest, forest edge and prairie communities, with the addition of some introduced species. With a few notable exceptions these birds tend to select community types which resemble the habitats that they originally occupied. Those native species which have invaded the edificarian insulae represent the greatest degree of habitat adjustment.

With progressive changes in the direction of proclimax, or with any intensification of human activity in the area, the species least likely to be affected adversely are those characteristic of the edificarian and subperennial insulae, and of the open and shrubby grassland.

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ECOLOGICAL STUDY OF VERNAL POOLS, SAN DIEGO COUNTY¹

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Vernal pools occur in heavy soil in areas of scanty rains on mesas and terraces north and east of San Diego and in other localities, chiefly in the cismontane region of southern California. The pool bottoms exist as a highly specialized and unique plant habitat and support a flora distinct from that of the surrounding areas. North and east of the city of San Diego is the Linda-vista mesa located in the foggy-desert belt of Russell ('31). A nearly level terrace, it is cut in a few places by gullies, but only where the mesa is flat and where there is no stream development are vernal pools present. This area, during the rainy season, presents thousands of these pools filling the small depressions of the mesa, intercepted throughout by low, rounded hummocks. Ellis ('19) states that the formation of the hummocks is due "to the action of the wind as it sweeps through the sparse desert vegetation and blows away the loose soil except where it is held by plant roots." Barnes (1879) attributes the formation of hummocks to water and wind action, and, to some extent to gophers, as well as to the absence of forests. Excavations made into the soil of pool bottoms show no stratification. As water in the pools is from the mesa-top only it carries little sediment, consequently, the pools are not being filled with silt. During the wet season when the hills and mesas are green with herbage, wind cannot reach the surface to pick up soil particles. Only during the dry summer and early autumn months can the fine particles be picked up from the pool bottoms and deposited against the bases of the shrubs on the hummocks, thus making them higher.

SOIL

The mesa is covered with reddish-brown or light-red to red loam with well-rounded particles of hard, resistant rocks, mainly quartzitic. Holmes ('18) states, "The surface soil usually gives way at a depth of about eight to eighteen inches to a thin layer of exceedingly compact clay loam or clay, which bakes hard and checks upon exposure during dry periods." Below this layer is reddish or brownish hardpan.

Most of the soil is fine, but, scattered here and there are bottoms with a surface largely of rounded stones and small boulders. The loss of water

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downward into this type of soil is slight due to the water-holding character of the soil. These pool bottoms form a peculiar habitat, distinct from ponds where sediment is deposited in quantities.

WATER

The water of the pools is obtained directly from precipitation and from the run-off of the mesa immediately adjacent to them, and not from distant elevations. Precipitation is meager, averaging 9.8 inches per year, the greater part coming during the months from October to April.² The depressions fill

TABLE I. *Monthly totals of precipitation*

1934	Sept.	.18	
	Oct.	.42	
	Nov.	1.95	
	Dec.	3.38	depressions with water
1935	Jan.	2.15	
	Feb.	4.54	
	March	1.42	many depressions dry
	April	1.02	all depressions dry
	May	.02	
	June	0	
	July	T	
	August	.18	
	Sept.	.01	
	Oct.	.05	
	Nov.	.07	
	Dec.	.74	
1936	Jan.	.75	
	Feb.	5.18	depressions with water
	March	.92	depressions dry
	April	.48	
	May	T	
	June	.01	
	July	.01	
	August	.28	
	Sept.	.04	
	Oct.	1.86	
	Nov.	.44	
	Dec.	4.45	all depressions with water
1937	Jan.	1.52	frost
	Feb.	4.22	
	March	2.65	
	April	.13	most depressions dry
	May	.32	all depressions dry by end of month
	June	.01	
	July	.16	
	August	0	
	Sept.	T	
	Oct.	T	
	Nov.	.02	
	Dec.	1.06	depressions with water for brief time
1938	Jan.	0.89	many depressions dry
	Feb.	3.26	depressions with water
	March	3.73	
	April	0.44	most depressions dry
	May	0.35	all depressions dry

² Report of U. S. D. A. Weather Bureau, San Diego.

with the first heavy rain, usually retaining some water until March or April, while the soil may remain moist until May in some of the deeper sections. In 1934-5 the first precipitation sufficient to fill the pools was in December, 1934; water did not fill the depressions again until February of 1936; in the succeeding season, pools filled in December of 1936, while in 1937 the pools obtained some water in December, sufficient amounts did not follow to keep the pools filled. Table I gives the monthly totals of precipitation with notations when depressions were filled with water or were dry.

The temperature of the water varies, the minimum occurring in January of 1935, 1937 and 1938 and February of 1936. Ice formed on the pools during several nights of January, 1937, while the highest recorded temperature, 34° C. was in April. Daily temperatures also vary considerably, the water being decidedly warm to the touch in the afternoons due to the shallowness of the pools.

Acidity was tested weekly in twenty-five pools during one season. Both the Quinhydrone-calomel electrode assembly with a Leeds and Northrup potentiometer³ and the La Motte set were used. There were variations from pH 5.6 early in March to 7.18 in April, with the majority of the readings between pH 6.13 and 6.55. Since there is practically no run-off there is a tendency for the pools to be acid, due to the accumulation of organic matter.

With the first heavy rains the pools are filled with water and more or less interconnect. After the first run-off from the mesa the pools, almost continuous between the hummocks, soon become reduced in size, the water being retained in what is often referred to as "hog-wallow" depressions, or vernal pools. These vernal pools consequently have an origin and physical character very different from other low, wet areas, such as small ponds or mudholes filled by streams, springs or seepage.

The areas are more or less oval in shape, with the long axis of the pool usually in a north-south direction, but there are many exceptions. In one hundred pools measured there was found a variation in area of from 22 by 35 meters to one less than a square meter. A large number measured between 10 by 15 meters and 3 by 5 meters. The deepest portion of the pools is usually their center where water in the larger pools stands at 25 to 30 centimeters for the first weeks after a rain, to 8 or 10 centimeters in smaller pools.

VEGETATION

The first information regarding the plants in these pools was briefly recorded by Orcutt in 1885 and again in 1887. The pool areas attract attention not only because they are a seasonal feature of the mesa-country but also because of their floristic specialization. Even in very dry years when the rainfall is much below normal, the pools remain delimited in the mesa vegetation and ruderals do not obliterate or greatly trespass their margins. Occasionally,

³ Tests made through the courtesy of Kyle F. Williamson, San Diego.

these latter plants may invade though they never establish themselves. The pools, it seems likely, are filled with water at the time that these common species of the mesa are beginning to grow on the surrounding areas, and, hence are too wet a habitat for them. The pool areas support a dense population of specialized plants whose seeds are well soaked before they sprout, whose roots are tolerant to water, slight acidity, water soaked ground and small oxygen supply, whose upper parts are not shade tolerant for the most part and whose period of growth to reach maturity is relatively short.

The following plants are commonly present in the vegetation of the vernal pools.⁴ Intruders able to grow in this specialized habitat but not restricted to it are marked *: *Pilularia americana* A. Br., *Isoetes howellii* Engelm. var. *minima* (A. A. Eaton) Pfeiffer, *I. orcuttii* A. A. Eaton, *Lilaea subulata* Humb. & Bonpl., *Phalaris lemmonii* Vasey, *Alopecurus saccatus* Vasey, *Deschampsia danthonioides* (Trin.) Munro var. *gracilis* (Vasey) Munz, *Eleocharis mamillata* Lindb. fil., **Juncus bufonius* L., *J. triformis* Engelm., *J. dubius* Engelm., **Brodiaea synandra* (Heller) Jeps., **B. orcuttii* (Greene) Baker, *Myosurus minimus* L. var. *apus* Greene, *M. minimus* L. var. *filiformis* Greene, **Lepidium nitidum* Nutt., *Sedum variegatum* Wats., *Tillaea aquatica* L., *T. drummondii* T. & G., *Callitriche marginata* Torr. var. *longipedunculata* (Morong) Jeps., *Elatine brachysperma* Gray, *E. californica* Gray, *Lythrum hyssopifolia* L., *Eryngium parishii* C. & R., *Centunculus minimus* L., **Gilia hamata* (Greene) Munz, *Plagiobothrys acanthocarpus* (Piper) Jtn., *P. leptocladus* (Greene) Jtn., *P. undulatus* (Piper) Jtn., *P. reticulatus* (Piper) Jtn. var. *rossianorum* Jtn., *P. bracteatus* (Howell) Jtn., *P. purerae* Jtn., *Acanthomintha ilicifolia* Gray, *Pogogyne nudiuscula* Gray, *P. abramsii* J. T. Howell, *Veronica peregrina* L. var. *xalapensis* (H. B. K.) Pennell, **Plantago hookeriana* F. & M. var. *californica* (Greene) Poe, *P. heterophylla* Nutt., *Downingia immaculata* Munz & Jtn., *Aplopappus venetus* (H. B. K.) Blake var. *decumbens* (Greene) Munz, *Psilocarphus tenellus* Nutt., *P. globiferus* (Bert.) Nutt., **Hemizonia fasciculatum* (DC.) T. & G., **Baeria chrysostoma* F. & M. var. *gracilis* (DC.) Hall, and *Cotula coronopifolia* L.

All the species are herbs, with the exception of one decumbent shrub, most of them are fragile and delicate, rarely reaching 15 centimeters in height. All those not starred are usually restricted to the pool bottoms except a few, as *Isoetes*, *Juncus*, etc., which may be present in ditches or other hydric locations close by. Certain species are found only in pools which hold water for long periods. No area has one dominant species, although a pool bottom may appear to have but one kind of plant, as *Downingia*, due to the density of its stand. With the passing of its maturity, however, other plants, as *Eryngium*, which have been in the seedling stage beneath the *Downingia* will grow and flower in the same space a few weeks later.

Perennials as *Juncus* and *Cotula* are found in the deeper portions of the larger pools. Annuals are largest in that portion where the water remains

⁴ Nomenclature as given in Munz's Manual of Southern California Botany, 1935.

the longest, those at the shallow edges frequently do not mature sufficiently to produce flowers.

A number of species present in pools on the Lindavista Mesa are also present in desiccating pools on mesas elsewhere in the county. Parish's ('17) list of vegetation of the Red Hill Pools, Riverside County, gives some of the same species as those in San Diego County. Orcutt (1887) states that he found "on the high mesa lands among the hills between the old missions of Santo Tomas and San Vicente, in Lower California, the same species of *Pilularia*, *Elatine*, *Isoetes*, *Tillaea* and *Callitriche* that I had previously collected on the mesas back of San Diego City." The author found these and other vernal pool species in pools near Ensenada, Lower California. In South America some of these species also appear in ephemeral pools on the highlands of Chile (Jaffuel, '32).

No comparative studies can be made of the vegetation of the vernal pools with that of ponds, for the mesas on which the pools are found do not have ponds or lakes. The plants present in ponds are species of *Salix*, *Populus*, *Baccharis* and other woody plants, *Polygonum* and other water plants. No vernal pool plants appear in any stages of the pond life. There is therefore in the vernal pool area a unique habitat with distinctly different plants from those encountered in pond studies.

Variation in the seasonal aspect is so noticeable that it is difficult from week to week to recognize a given depression. This is especially true in a season of small rainfall. In early spring, especially when there is an abundance of water, the algal population is considerable, and as the pools dry and the water level decreases, the seed plants push their way through a mass of algal filaments. Among the more abundant genera of algae are *Spirogyra*, *Zygnema*, *Microspora* and *Nostoc*. In addition, the ground is covered with liverworts, frequently submerged for a few weeks after heavy rains.

Callitriche is early found floating on the surface and as the water evaporates spreads out on the soil. *Isoetes* and *Pilularia* appear early in the season, and as they reach maturity plants of *Downingia*, *Plagiobothrys*, *Veronica*, etc., often growing below the water level, now develop leaves and flowers above the water surface. While *Plagiobothrys* is flowering, seedlings of *Pogogyne* begin to mature with its flowering season following that of *Plagiobothrys*, usually when the soil is dry. Meanwhile, the late flowering plants, as *Eryngium* have been spreading over the surface and when most of the other plants have withered, it matures on the hard, cracked soil, completing the growing season of the vernal pools. This is a simple explanation of a complicated succession of plants for temperatures of soil and water, amounts of water and other factors vary the conditions from season to season as well as in individual pools throughout the area.

In years that the rainfall is abundant the pools are luxurious with flowers; in dry years there is a paucity both in the kinds and numbers of plants. As most of the year the pool bottoms are dry the wind is able to blow the loose



FIG. 1. Aspect of vernal pools in winter (a) and in late spring (b).

soil particles and scatter the seeds of the pool plants. In addition, birds may play a part in seed distribution as they are frequently seen. Although the seeds of the pool plants are scattered beyond the confines of the pools, they do not grow on the mesa beyond the limits of the pool margins. As has been mentioned the water requirements of the pool plants are not found outside the pool areas.

TABLE II. *List quadrats*

Number of quadrat	Character of quadrat; date of count	Name of plant	No. per sq. meter
1	Center of pool; moist April 2, 1937	<i>Tillaea</i> , in flower	3300
		<i>Psilocarphus</i>	3100
		<i>Downingia</i> , in bud	1900
		<i>Pilularia</i>	1850
		<i>Isoetes</i>	1650
		<i>Callitriche</i> , in flower	450
		<i>Brodiaea</i>	90
2	Center; moist April 3, 1937	<i>Tillaea</i> , in flower	8500
		<i>Psilocarphus</i>	3800
		<i>Pilularia</i>	3200
		<i>Downingia</i> , in flower and bud	3100
		<i>Isoetes</i>	1800
		<i>Deschampsia</i> , in flower	90
		<i>Callitriche</i> , in flower	55
3	Center of deep depression; wet April 9, 1937	<i>Myosurus</i> , in flower	3200
		<i>Baeria</i> , dry spot	26
		Scattering of <i>Callitriche</i>	
4	Shallow; dry; cracked April 9, 1937	<i>Tillaea</i> , in flower	1100
		<i>Psilocarphus</i> , in flower	190
		Lichens	28
		<i>Juncus bufonius</i>	16
		<i>Plagiobothrys</i> , in flower	6
		<i>Callitriche</i> , dried	
5	Center of pool; damp April 16, 1937	<i>Tillaea</i> , in flower	4500
		<i>Pilularia</i>	3400
		<i>Psilocarphus</i>	252
		<i>Callitriche</i> , in flower	110
		<i>Plagiobothrys</i> , in flower	68
		<i>Lythrum</i>	40
		<i>Downingia</i> , in flower	32
		<i>Isoetes</i>	20
		<i>Deschampsia</i>	6
		<i>Hemizonia</i> , dry corner	2
		<i>Eleocharis</i> , in flower	2
6	Stony; dry April 16, 1937	<i>Isoetes</i> , dried	1200
		<i>Tillaea</i> , in flower	1100
		<i>Downingia</i> , immature; depauperate	700
		<i>Downingia</i> , in flower	360
		<i>Brodiaea orcuttii</i> , in bud	24
		<i>Deschampsia</i> , in flower	6
7	Water 8 cm. in depth April 17, 1937	<i>Psilocarphus</i> , drier corner	30
		<i>Pogogyne</i>	18
		<i>Lilaea</i> , in flower	16
		<i>Plagiobothrys</i> , in flower; drier corner	9
		Rest of quadrat a dense mat of <i>Isoetes</i> , <i>Pilularia</i> , covered with <i>Callitriche</i> and green algae	

TABLE II.—Continued

Number of quadrat	Character of quadrat; date of count	Name of plant	No. per sq. meter
8	Pastured; rocky; dry April 17, 1937	<i>Pogogyne</i>	850
		<i>Downingia</i> , in flower	510
		<i>Deschampsia</i> , in flower	18
		<i>Phalaris</i> , in flower	5
		<i>Eryngium</i>	1
		<i>Hemizonia</i>	1
		Weedy grasses (<i>Hordeum</i> and <i>Bromus</i>)	23
9	Just north of burned quadrat No. 24; slightly stony; damp April 19, 1937	<i>Isoetes</i>	3110
		<i>Psilocarphus</i> , in flower	2880
		<i>Eleocharis</i> , in flower	255
		<i>Downingia</i> , in flower	180
		<i>Plagiobothrys</i> , in flower	80
		<i>Pogogyne</i>	60
10	Damp; stony April 19, 1937	Pure stand of <i>Pogogyne</i> except for	
		<i>Deschampsia</i> , in flower	8
		<i>Brodiaea</i>	5
11	Dry; stony April 19, 1937	Pure stand of <i>Pogogyne</i> except for	
		<i>Downingia</i>	2
12	Moist; center of deep depression April 19, 1937	<i>Isoetes</i>	1600
		<i>Downingia</i> , in flower	1500
		<i>Psilocarphus</i> , in flower	450
		<i>Eleocharis</i> , in flower	400
		<i>Deschampsia</i> , in flower	110
		<i>Tillaea</i> , in flower	45
		<i>Plagiobothrys</i> , in flower	45
		<i>Lythrum</i>	10
		<i>Cotula</i> , in flower	1
13	Damp April 20, 1937	<i>Callitriche</i>	900
		<i>Isoetes</i>	900
		<i>Psilocarphus</i> , in flower	440
		<i>Tillaea</i> , in flower	310
		<i>Downingia</i> , in flower	93
		<i>Brodiaea</i>	31
		<i>Eleocharis</i> , in flower	29
		<i>Eryngium</i>	15
14	Edge of depression; dry; small stones April 20, 1937	<i>Callitriche</i>	700
		<i>Isoetes</i>	350
		<i>Myosurus</i> , in flower	200
		<i>Psilocarphus</i> , in flower	90
		<i>Tillaea</i> , in flower	80
		<i>Eryngium</i>	17
		<i>Brodiaea</i>	10
		<i>Eleocharis</i> , in flower	4
15	Edge of depression; dry April 22, 1937	<i>Juncus triformis</i> , in flower	1500
		<i>Psilocarphus</i> , in flower	1500
		<i>Downingia</i> , in flower	1050
		Liverworts	800
		<i>Tillaea</i> , in flower	450
		<i>Brodiaea</i>	280
		<i>Eleocharis</i> , in flower	56
		<i>Callitriche</i> , in flower	55
		<i>Eryngium</i>	11

TABLE II.—*Continued*

Number of quadrat	Character of quadrat; date of count	Name of plant	No. per sq. meter
16	Deep pool; water April 22, 1937	<i>Eryngium</i>	28
		<i>Eleocharis</i> Rest a mass of green algae and <i>Callitriche</i> in water with <i>Isoetes</i> in mud	9
17	Deep pool; water April 22, 1937	<i>Downingia</i> , in flower	280
		<i>Juncus dubius</i> , in flower Rest a floating mass of green algae; some <i>Callitriche</i> ; in mud hun- dreds of <i>Isoetes</i> plants	18
18	Edge of depression; dry; somewhat stony April 24, 1937	<i>Isoetes</i> (moister corner) withering	4040
		<i>Tillaea</i> , in flower	1170
		<i>Psilocarphus</i> , in flower	1110
		<i>Downingia</i> , in flower	300
		<i>Pogogyne</i> , in flower	270
		<i>Deschampsia</i> , in flower	150
		<i>Veronica</i> , in flower	120
		<i>Eleocharis</i> , in flower	58
		<i>Eryngium</i>	18
		<i>Brodiaea</i>	15
19	Center; wet April 24, 1937	<i>Hemizonia</i> , drier corner	2
		<i>Isoetes</i> , much withered	6000
		<i>Pilularia</i>	2200
		<i>Downingia</i> , in flower	500
		<i>Pogogyne</i> , in flower	280
		<i>Callitriche</i> Algae	
20	Edge; damp April 24, 1937	<i>Downingia</i> , in flower	1200
		<i>Pilularia</i> , withering	600
		<i>Isoetes</i> , withering	600
		<i>Deschampsia</i> , in flower	40
		<i>Veronica</i> , in flower <i>Callitriche</i>	40

POPULATION STUDIES

In making a population study, the list, permanent and denuded quadrats were employed. A square meter, divided into smaller squares was used and in some cases where the vegetation was very dense 10, 20 or 50 square decimeters scattered over the square meter were used and the total computed. Difficulty was encountered in determining an individual plant especially in the cases of *Pilularia* and *Callitriche*. Pools were selected in varied portions of the mesa.

Twenty-five permanent quadrats marked with tags were checked during the spring of 1936 and 1937. There was a great increase in the density of the stands in 1937 as compared to 1936 and 1938, the number being frequently double. Hundreds of plants in marked quadrats never matured in 1936. *Isoetes*, *Pilularia* and the green algae were much more abundant in

TABLE III. *Denuded quadrats*

Number of quadrat	Character of quadrat; date of count	Name of plant	No. per sq. meter
21	Top soil removed to depth of 5 cm.; damp April 1, 1937	<i>Callitriche</i>	pure stand
22	Top soil removed to depth of 5 cm.; damp April 9, 1937	<i>Lythrum</i> <i>Callitriche</i> , rest of quadrat	3
23	Top soil removed to depth of 3 cm.; rather dry April 16, 1937	<i>Downingia</i> , in flower <i>Brodiaea</i> <i>Lythrum</i> $\frac{1}{3}$ of quadrat (deep portion) covered with <i>Callitriche</i>	17 8 2
24	Burned previous season; slightly stony; damp; just south of quadrat No. 9 April 19, 1937	<i>Tillaea</i> , in flower <i>Downingia</i> , in flower <i>Psilocarphus</i> , in flower <i>Pogogyne</i> <i>Callitriche</i> , small amount	1440 6 1 1
25	Top soil removed to depth of 5 cm.; damp April 20, 1937	<i>Downingia</i> , in flower <i>Brodiaea</i> <i>Callitriche</i> sparsely scattered on damp soil	8 3
26	Burned previous season; damp April 26, 1937	<i>Tillaea</i> , in flower <i>Psilocarphus</i> , in flower <i>Brodiaea</i> <i>Hemizonia</i> <i>Downingia</i> , in flower	82 32 18 14 8
27	Top soil removed to depth of 3 cm.; dry April 26, 1937	<i>Tillaea</i> , in flower <i>Psilocarphus</i> , in flower	2600 44
28	Top soil removed to depth of 8 cm.; moist April 26, 1937	<i>Downingia</i> , in flower <i>Brodiaea</i> Scattering of <i>Callitriche</i>	10 2
29	Top soil removed to depth of 3 cm.; dry April 26, 1937	<i>Brodiaea</i> <i>Downingia</i> , in flower <i>Callitriche</i>	16 11
30	Top soil removed to depth of 3 cm.; deep pool; moist April 26, 1937	<i>Brodiaea</i> <i>Lythrum</i> Abundant with <i>Callitriche</i>	8 1
31	Top soil removed to depth of 3 cm.; dry April 26, 1937	<i>Lythrum</i> <i>Callitriche</i>	18
32	Top soil removed to depth of 5 cm.; dry April 26, 1937	Pure stand of <i>Callitriche</i>	

1937. In pastured areas there was an increase in grasses, especially weedy grasses and non-pool plants. Low plants as *Isoetes* or *Pilularia* were not cropped, but *Downingia* and other larger annuals were eaten closely in 1936 as the mesa grasses withered early in the season. In grazed areas in 1936 less than half as many plants appeared as in 1935, but in the same area not pastured in 1937 there was about 40 per cent increase in the number of plants.

Chart quadrats were made of shallow depressions in 1936 but so much vegetation appeared in these same areas in 1937 that the work was too difficult and was not continued.

No two quadrats are alike, either as to the density of the stand or as to the components of the vegetation. In 1937 the stands were much denser than in 1935 or 1936; the plants were taller and many more plants reached maturity. The count is low where large sized plants predominate, where the pool bottom is stony or where the water remains for a very short period.

First to appear in a pool where previously three to eight centimeters of top soil had been removed is *Callitriche*. There are fewer green algae than in undisturbed pools. The *Callitriche* is soon crowded by *Downingia* and other annuals. Occasionally, plants of *Brodiaea* appear in the shallower pools or at their margins, for their corms buried deeply in the soil were not disturbed when the top soil was removed. In a quadrat denuded by burning the most conspicuous plant is *Tillaea* with a sprinkling of other annuals.

Zonation is varied in that no two pools have the same depth, nor is the depth uniform throughout. Twenty-five pools were tagged and measurements of length, width and depth of the water were taken weekly during one season to check on the zonation, if possible. This was difficult as a heavy rain would increase the depth of the water, inundating plants which ordinarily would not be submerged. The zoning of the pools is not as conspicuous as in pond studies, due to the smallness of the areas treated, the irregularity in amounts of precipitation, the unevenness in depth of the water and to the smallness of the plants. The zonation is not spacial as in pond studies but rather in this case, temporal, i.e. seasonal. A single species does not, as a rule, form a pure stand, nor are any two or more given pool species found regularly associated together. Then, too, a depression may be moist enough for *Isoetes* and *Pilularia* and then dry quickly leaving barely visible plants on the ground, while *Downingia* and others will be flowering above them. In the deeper sections where water stands to a depth of twenty-five centimeters for a few weeks, we find perennials as *Juncus*, *Cotula*, *Eryngium* and *Eleocharis*. The water may be clear, but it is usually covered with *Callitriche* and green algae. In portions slightly shallower there are present *Isoetes*, *Pilularia*, *Elatine* and *Myosurus*. *Psilocarphus*, *Tillaea*, *Veronica* and *Pogogyne* are scattered between the deeper portions and the margins. Around the shallow edges are *Plagiobothrys* and *Deschampsia* and in the driest portions at the margins are grasses and other mesa plants, invaders from

the surrounding areas. Liverworts are abundant in early spring in the moist areas; lichens on some of the dry spots.

GERMINATION STUDIES

From early November to February 1937-8 twenty soil samples from vernal pool bottoms, mesa soil nearby and subsoil were placed in 7 by 10.5 inch trays, covered with two centimeters of water and kept in a sunny location. Temperature ranges were 16° to 33° C. In four days some plants appeared, the maximum number within a month. The highest count was 305 dicotyledons and 40 monocotyledons in one tray. After trays were permitted to dry out thoroughly they were again flooded and the highest count was 145 young plants in the tray just mentioned above. The trays containing soils from the mesa around the pool had but a small percentage of plants and they soon died. Trays with subsoil had as many as 145 dicotyledons and three dicotyledons. Algae appeared in most of the trays, also some liverworts. Undoubtedly, many seeds of mesa plants find in the pools conditions unsuitable for growth. Soil from the surface of the pool bottom had the highest percentage of plants, with *Downingia* predominating.

ACKNOWLEDGMENTS

The author wishes to take this opportunity to express her appreciation to Dr. Ivan M. Johnston of Arnold Arboretum, Harvard University, for suggesting this interesting ecologic study and his subsequent interest in the investigation and criticism of the manuscript. Also, to Dr. Philip A. Munz for his interest and kindness in identifying specimens.

SUMMARY

Vernal pools on mesas in various portions of San Diego County are abundant on the Lindavista mesa in the foggy-desert belt, with scant seasonal winter rains. With exposure to full sun, the daily and seasonal fluctuations in the temperature of the water are high as the pools are small and shallow. Within a few months' period the pool bottoms present a rapid change from hydric to extreme xeric conditions.

The flora of the pools is distinct from that of the surrounding areas. No trees or shrubs (except one decumbent one) are present; there are few perennials; annuals are most numerous. The plants are mostly fragile and delicate, less than fifteen centimeters in height.

The seasonal aspect is very noticeable. At first *Callitriche* and green algae are abundant, then *Juncus* and *Eleocharis* become conspicuous along with *Pilularia* and *Isoetes* which grow in mud or somewhat submerged. Then *Downingia*, *Plagiobothrys* and *Psilocarphus* appear, then *Pogogyne* followed by *Eryngium* growing in the caked dry soil.

List quadrat studies show very dense populations in favorable portions

of a pool and as low as fifty plants per square meter in other portions. Variation depends principally on the amount of water present, on whether the area has been denuded or not, and on the types of plants present. Permanent quadrats show great differences in yearly appearance due to amounts of precipitation and also to grazing.

Zonation is not noticeable. Perennials are present in the deeper portions, while annuals are usually found where it is shallower. Along the margins may be found invaders from the surrounding mesa. *Callitriche* and green algae frequently cover the surface of the water. Liverworts are abundant on wet soil.

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EXPERIMENTS ON THE NUTRITION OF ZOOTERMOPSIS. III. THE ANAEROBIC CARBOHYDRATE DISSIMILATION BY THE INTESTINAL PROTOZOA¹

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The researches of Cleveland ('24), Trager ('32) and Hungate ('38) have established that the termite, *Zootermopsis*, is dependent upon its intestinal protozoa for the digestion of a large part of the carbohydrate material necessary to satisfy its energy requirements. Most of the carbohydrates (cellulose and hemicellulose) utilized in the termite are digested by the protozoa. Glucose, which has been shown to be the end product of this digestion (Trager, '32) has usually been postulated as the material liberated by the protozoa and absorbed by the termite (Trager, '34).

Another hypothesis as to the nature of the materials liberated by the protozoa and absorbed by the termite is as follows: The protozoa in the alimentary tract digest the carbohydrates of wood to glucose (other simple sugars may also result) and then utilize the glucose in an anaerobic metabolism. The products of this metabolism are absorbed by the termite and further oxidized to carbon dioxide and water.

The large size of the damp-wood termites, *Zootermopsis nevadensis* and *Z. angusticollis*, and the profusion with which the protozoa occur in them have made it feasible to obtain enough of the intestinal protozoa so that the above hypothesis could be tested by a study of their carbohydrate metabolism. Termites were collected in the vicinity of Pacific Grove, California, taken to the laboratory, and their gut contents utilized for most of the following experiments. For some experiments termites maintained in laboratory cultures at Austin, Texas, were used.

For the use of space and equipment in the microbiology laboratory of the Hopkins Marine Station and for many helpful suggestions the author is deeply indebted to Dr. C. B. van Niel.

EXPERIMENTAL

A. Evidence that the protozoa carry on an anaerobic metabolism

Experiment 1.

The anaerobic nature of the protozoa in the gut contents was first tested. Three hanging drop culture chambers were prepared as indicated in figure 1.

¹ This research has been aided in part by a grant from the American Association for the Advancement of Science.

Moist cotton was placed on the walls of the chamber and the top of the upright cylindrical portion was ground smooth so that a small piece of glass slide could be sealed on with stopcock grease to make an airtight connection which would not leak under a vacuum.

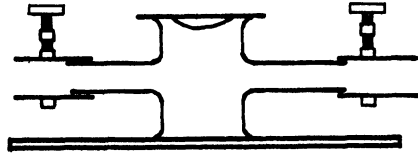


FIG. 1. Hanging-drop culture chamber.

In conducting the experiment the glass slide which formed the top of each chamber was removed and the ground glass surface ringed with grease. A hanging drop of the undiluted hind-gut contents of an individual of *Zootermopsis* was placed on the slide and the latter immediately inverted over the top of the culture chamber. Oxygen was passed through number 1 and air through number 2, the gas being permitted to flow for about ten seconds before the chamber was sealed off. Culture number 3 was evacuated and sealed off, leaving a partial vacuum of about 4 cm. mercury pressure. The protozoa in all the cultures were examined from time to time. In the oxygen culture most of them were dead in 15 minutes, they were dead in one hour in the air culture, but lived for over 6 hours in the evacuated culture.

The experiment was modified by putting a yeast suspension in the bottom of all three culture chambers to provide slightly more anaerobic conditions. In this experiment the protozoa lived for 21 minutes in oxygen, one and one-half hours in air, and seven and one-half hours in the evacuated cultures. In both experiments the correlation between oxygen tension and speed of death indicates that oxygen is toxic to the termite protozoa.

In another test a few individuals of *Trichonympha sphaerica* remained alive and active for as long as 38 days in a depression slide which was maintained completely anaerobic by adding a dense suspension of yeast cells to Trager's culture medium and excluding air with a cover slip ringed with vaseline. This further demonstrates the anaerobic nature of the protozoa in agreement with the observations of Trager ('34).

In the termite the protozoa apparently are able to survive because the host tissues keep the oxygen supply below a lethal concentration. Increase of the oxygen pressure as in defaunation methods (Cleveland, '25) operates to kill the protozoa even in the protecting environment of the termite.

Experiment 2.

The hind-gut contents of *Zootermopsis* were tested in a Warburg respirometer for gas and acid production under anaerobic conditions. Most of the protozoa were removed from two grams of termites by squeezing the gut contents into a small test tube completely filled with a solution obtained by

mixing 20 cc. of 0.126 per cent NaHCO_3 , 0.1 per cent NaCl , and 0.05 per cent KCl with 2 cc. of 0.01 molar HCl containing 0.1 per cent CaCl_2 . Loeffler's dehydrated blood serum (0.1 per cent) was also added. As each drop of gut contents was squeezed out it sank quickly to the bottom of the tube, thus coming in contact with a minimum of oxygen. After all the gut contents were added they were thoroughly mixed with the medium and the large protozoa were then allowed to settle. These large protozoa of the genus *Trichonympha* (Kirby, '32) are present in far greater volume than the smaller protozoa (*Trichomonas*, *Streblomastix*, *Hexamastix*, *Tricercomitus*) and the bacteria. The small protozoa and the bacteria in the supernatant fluid were drawn off, 100 mg. of finely divided cellulose (prepared according to Farr and Eckerson, '34) were added, and more of the medium was added to make 4 cc. This suspension containing most of the bacteria and the small protozoa was divided between two Warburg vessels.

The large protozoa were similarly made up to 4 cc. after the addition of 100 mg. of cellulose and were divided between two vessels. The vessels were attached to the manometers and placed in the water bath at 26.8°C . They were then equilibrated with a mixture of 95 per cent nitrogen-5 per cent carbon dioxide. After temperature equilibrium was reached the manometers were read and then the acid in the side arm of vessels 17 and 19 (see table I) was added to the protozoan suspension. This killed the protozoa and freed the carbon dioxide present as bicarbonate in the medium. By reading the increased pressure the carbon dioxide present as bicarbonate in the suspension at the beginning of the period of measurement could be calculated.

TABLE I. Gas and acid production by the gut contents of *Zootermopsis*

Vessel	16	17	18	19
Contents	Suspension of large protozoa		Suspension of small protozoa and bacteria	
In side arm	Acid at end	Acid at beginning	Acid at end	Acid at beginning
Gas produced, cmm./gm. hr.	124		21	
CO_2 liberated by acid prod. cmm./gm. hr.	119		18	

Readings were made on the other manometers at frequent intervals for two hours and then the acid in vessels 16 and 18 was added, giving the total gas pressure in these vessels at the end of the period. The total gas in vessel 16 minus that in vessel 17 gave the amount of gas produced by the large protozoa in two hours. The total gas in vessel 18 minus that in 19 gave the amount of gas produced by the small protozoa and the bacteria. In vessels 16 and 18 the pressure increase during the two-hour period was due to production of gas in metabolism plus liberation of carbon dioxide from the bicarbonate through acid production. The carbon dioxide liberated by acid production was obtained by subtracting the amount of gas formed in metabo-

lism from the total gas appearing during the experiment. It was assumed that all of the gas formed in metabolism was carbon dioxide and the vessel constant for carbon dioxide was used in converting pressure changes into cubic millimeters. As will be seen, not all of the gas was carbon dioxide, but since the volume of liquid in all of the flasks was less than one-tenth the volume of the gas phase and since carbon dioxide was found to be the principal constituent of the gas the error involved is considerably less than ten per cent. The figures for the amount of gas are a little too high.

Since the suspension containing the large protozoa produced much more gas and acid than did the suspension of small protozoa and bacteria these products may be ascribed to the large protozoa. The similarity between the ratios of gas production to acid production in vessels 16 and 18 suggests that the metabolism of the small protozoa and bacteria results in products similar to those of the large protozoa.

Relatively smaller amounts of gas and acid have been formed by the small protozoa and bacteria in other similar runs and so the metabolism of these organisms has been disregarded in most experiments. The entire gut contents have usually been used without attempting to measure separately the metabolism of the small protozoa and bacteria. In experiments run for as long as four hours there was no evidence of an increasing fermentation which might be interpreted as due to the multiplication of bacteria utilizing the metabolic products of the protozoa. Where runs were long continued the protozoa gradually died and the production of gas and acid always fell off.

B. The nature of the acid produced

Experiment 3.

The protozoan suspension in vessel 16 of the preceding experiment was tested for volatile acids as follows: The suspension was acidified with H_2SO_4 and steam distilled, the steam being passed first through the suspension, then through 2 cc. of 0.01 normal NaOH before going to the condenser. The flasks containing the suspension and the alkali were heated with a small flame to prevent condensation of steam in them. The distillation was continued until 70 cc. of water had collected in the receiving flask of the condenser. The NaOH was then titrated with 0.01 normal HCl in an atmosphere rendered free of carbon dioxide by bubbling carbon dioxide-free air through the vessel. Brom thymol blue was used as the indicator.

The protozoan suspension in vessel 17 was similarly treated as a check for volatile acids in the suspension at the beginning of the Warburg run and for volatile acid in the water used to generate steam. When the protozoan suspension in vessel 16 was treated 0.0042 milliequivalents of acid were needed to neutralize the alkali, whereas 0.0134 milliequivalents were needed in vessel 17. This indicates the presence of volatile acids to the extent of 0.0092 milliequivalents. This amount of acid would liberate 206 cubic millimeters of carbon dioxide from a bicarbonate solution. Since in vessel 16 the protozoa

from one gram of termites metabolized for a period of 2 hours the volatile acid produced per gram of termites per hour would liberate 103 cubic millimeters of carbon dioxide. This constitutes 85 per cent of the total acid (equivalent to 119 mm. carbon dioxide) produced. In four comparable experiments the volatile acid was found to be 62, 85, 85, and 82 per cent, respectively, of the total acid.

Experiment 4.

The gut contents were squeezed out of 0.7 gm. of termites into a glass-stoppered test tube containing finely ground cotton particles suspended in Trager's ('34) solution U from which the bicarbonate was omitted. The culture medium was evacuated with a water pump before the protozoa were added and the tube was completely filled with the suspension containing the protozoa. On examination of a drop of the suspension after 5 hours all of the protozoa appeared to be alive, active, and filled with cellulose. After 17 hours more than half of the protozoa were still alive and active though the presence of many dead ones indicated that conditions had become unfavorable. The pH was 6.1. It was adjusted to 7.2 with NaOH and the mixture was then evaporated to about 3 cc. The residue was acidified and the volatile acids steam distilled as in experiment 3. Volatile acid amounting to .044 milliequivalents was present. It was freed by the addition of an equal amount of sulphuric acid and a Duclaux distillation was performed. The points obtained by titration of various fractions of the distillate have been plotted as circles in figure 3. The neutralized distillates were concentrated by boiling, the acids again freed by the addition of H_2SO_4 and most of the liquid distilled over, .03 milliequivalents of volatile acid being titrated in the distillate. The acid was freed with H_2SO_4 and used in a second Duclaux distillation which gave the points shown as crosses in figure 2. For purposes of comparison the curves for formic, acetic, and propionic acid are also shown. These latter were experimentally determined in the same apparatus with quantities of the pure acid about equal in amount to the unknown. The identity of the first and second distillation curves of the volatile acid from the protozoa culture with that of acetic acid suggests that the two acids are the same. The similarity between the first and second curves indicates that a pure acid rather than a mixture was present.

Experiment 5.

Further information on the nature of the acid was obtained in another experiment. The gut contents from 3.66 gm. of *Z. angusticollis* were mixed in a Carrel flask with 12 cc. of a solution containing 0.084 per cent sodium bicarbonate, 0.1 per cent sodium chloride, 0.05 per cent potassium chloride, 0.01 per cent $CaCl_2$, 0.001 molal HCl, 0.1 per cent Loeffler's blood serum, and 86 mg. of finely shredded filter paper. After 14 hours most of the protozoa were dead. The suspension was steam distilled into a solution of

NaOH, H_2SO_4 being used to titrate the excess alkali. The amount of acid used in titration indicated that 0.085 milliequivalents of volatile acid were present.

The acid was freed by the addition of 0.085 milliequivalents of H_2SO_4 and the solution distilled almost to dryness. By adding 0.055 milliequivalents

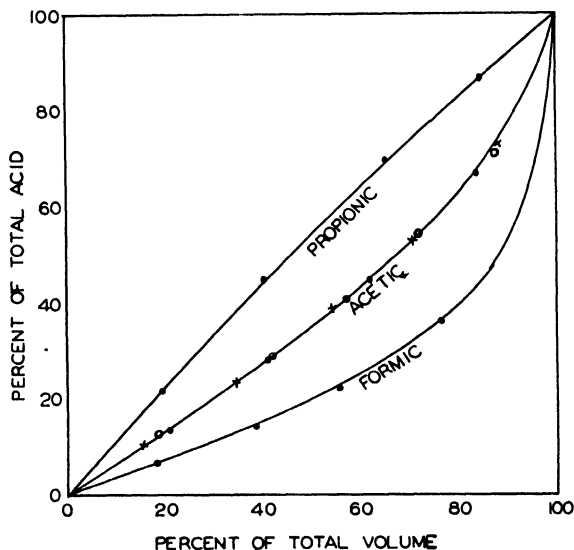


FIG. 2. Distillation curves for the volatile acid of the protozoa and for several known acids.

of $\text{Ba}(\text{OH})_2$ the distillate was brought to a pH of 6.0, a glass electrode being used to determine the acidity. A very slight amount of BaSO_4 forming on addition of the $\text{Ba}(\text{OH})_2$ was filtered off. The filtrate containing the barium salt of the volatile acid was collected in a 50-cc. beaker and evaporated to dryness over a water bath; the residue was taken up in a few drops of warm water; transferred to a weighed centrifuge tube and evaporated to dryness. The weight of the dried salt was found to be 6.38 mg. A few drops of warm water were added and the barium was precipitated with a solution of sodium sulphate. The precipitate was separated by centrifuging and was washed several times. The tube was then dried and weighed. The BaSO_4 amounted to 5.72 mg. The barium thus constituted 52.8 per cent of the unknown. The theoretical value for $\text{Ba}(\text{C}_2\text{H}_3\text{O}_2)_2$ is 53.7 per cent, for $\text{Ba}(\text{C}_3\text{H}_5\text{O}_2)_2$ it is 48.5 per cent, for $\text{Ba}(\text{CHO}_2)_2$ 60.4 per cent. The percentage of barium in the unknown salt agrees most closely with that of barium acetate. This agrees with the evidence obtained from the Duclaux distillations.

The volatile acid from another run was collected in a watch glass and a few crystals of sodium uranyl carbonate were added. As the water evaporated the characteristic tetrahedral crystals of sodium uranyl acetate formed in profusion.

It may be concluded that the volatile acid produced by the protozoa is principally acetic acid.

C. The nature of the gas produced

Experiment 6.

In order to reduce the carbon dioxide evolution caused by acid production the bicarbonate in Trager's solution U was omitted. This left a solution consisting of 0.2 per cent NaCl, 0.15 per cent sodium citrate, 0.18 per cent KH_2PO_4 , 0.008 per cent CaCl_2 , 0.005 per cent MgSO_4 , and 0.1 per cent Loeffler's blood serum. By adding NaOH the pH was adjusted to 7.7.

The hind-gut contents were removed from 2.3 gm. of *Z. angusticollis* and suspended in 8 cc. of the above medium with the addition of 200 mg. of finely divided cellulose. The pH of this mixture was 7.3. The suspension was equally divided between 2 respirometer vessels and oxygen-free nitrogen was passed through them after they were placed in the bath. Pressure changes were followed for a period of one hour. The total pressure changes in terms of millimeters of Brodie solution were as follows:

Vessel	Pressure	Side arm contents
16	22.7 mm.	KOH
17	18.6	"
18	62.5	H ₂ O
19	69.7	"

Since the volume of all these vessels was between 23.3 cc. and 25.7 cc. it is evident even without correction with vessel constants that much more gas was liberated in vessels 18 and 19 than in 16 and 17. Evidently most of this gas was carbon dioxide. But the very definite evolution of gas in vessels 16 and 17 containing KOH indicated that another gas was also concerned. It seemed probable that this other gas was either hydrogen or methane.

Experiment 7.

In order to test for hydrogen production an absorbent composed of a 10 per cent aqueous solution of methylene blue in platinized asbestos was employed. It was prepared by placing asbestos containing 5 per cent platinum in a sintered glass filter and covering it with the solution of methylene blue. The excess solution was removed by suction, leaving the platinized asbestos impregnated with the methylene blue. While still moist a portion of it was placed in the side arm of the respirometer vessel as a hydrogen absorbent. Six vessels were prepared as follows:

Vessel	16	17	18	19	20	21
Volume in cc.	25.7	25.6	24.9	23.3	25.7	26.3
In vessel	1.8 cc. of a protozoan suspension	-----	-----	-----	1.8 cc. water	-----
In 1st arm	0.2 cc. water	-----	ca. 0.2 cc. hydrogen absorbent	-----	-----	-----
In 2nd arm	0.2 cc. KOH	-----	-----	-----	-----	-----

Vessels 20 and 21 served as a check for the possible presence of hydrogen in the gas used to fill the manometers. This was thought necessary since the oxygen was removed by passing the gas over hot copper which had previously been reduced with hydrogen. The oxygen-free nitrogen was passed through all the vessels and after temperature equilibrium was reached readings were taken at 10 minute intervals. The pressure changes are shown in figure 3.

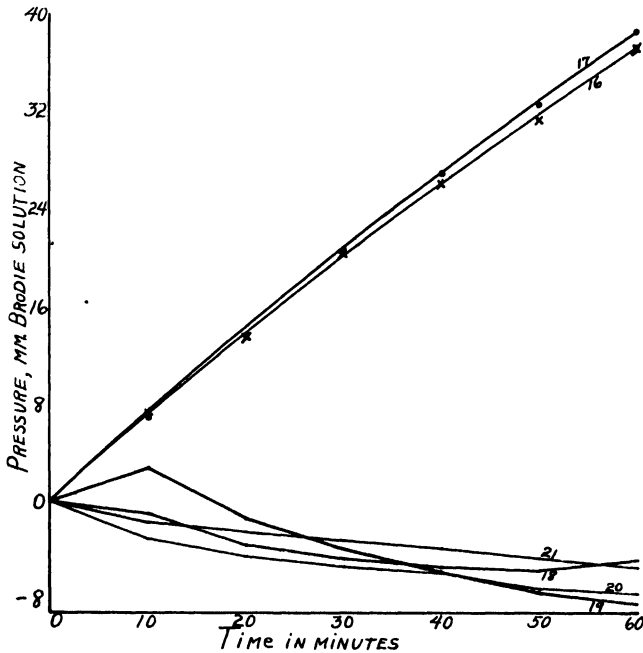


FIG. 3. Hydrogen production by a suspension of the gut contents of *Zootermopsis*.

At the end of the experiment the methylene blue in vessels 18 and 19 was noticeably lighter in color than at the beginning of the experiment, indicating a conversion of the methylene blue to the reduced form. The methylene blue in vessels 20 and 21 retained its original color. This experiment indicates that, in addition to carbon dioxide, hydrogen is produced by the protozoa in *Zootermopsis*. The author is unable to account for the slight negative pressures developing in vessels 18 to 21. If it were due to the absorption of oxygen, carbon dioxide, or hydrogen, it would not be expected to continue for so long.

Experiment 8.

Since hydrogen is a common product of an anaerobic metabolism in bacteria it seemed desirable to perform another experiment in which the small protozoa and bacteria were tested and their hydrogen production compared with that of the large protozoa. The small protozoa and bacteria were

separated from the large protozoa by sedimentation as in experiment 2. Vessels were prepared as follows:

Vessel	16	17	18	19
In side arm	0.2 cc. KOH	0.2 cc. H ₂ O ³	0.2 cc. KOH	0.2 cc. H ₂ O
Vessel contents	2 cc. of a suspension of large protozoa		2 cc. of a suspension of small protozoa and bacteria	

³ In a separate experiment the binding of carbon dioxide by the phosphate medium was found to be small.

The results obtained are shown in figure 4.

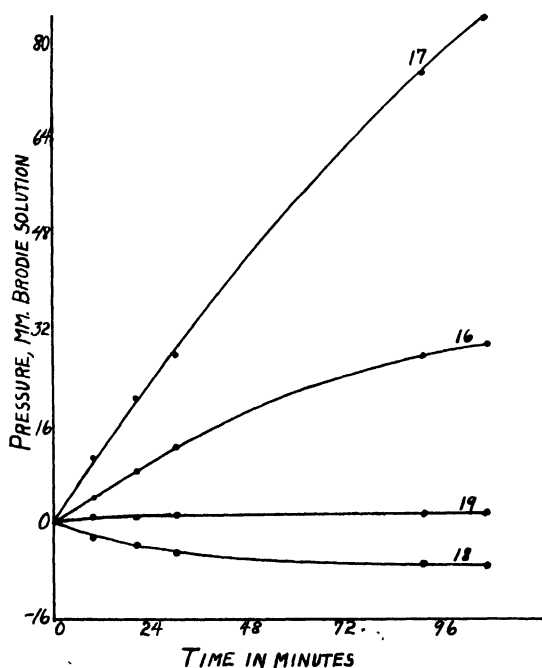


FIG. 4. Hydrogen and carbon dioxide production by suspensions of the large protozoa and suspensions of the small protozoa and bacteria.

The absence of any evolution of gas in vessel 18 as compared with vessel 16 indicates that hydrogen production is linked with the presence of the large protozoa rather than with the small protozoa and bacteria in the gut.

D. The metabolic products of the protozoa within the termite

Experiment 9.

Randall and Doody (in Kofoed *et al.*, '34) remark about *Zootermopsis*, "When the gut contents were acidified there was always a strong odor of acetic or similar organic acid of low molecular weight. This hints strongly at the production of acetates or butyrates in the digestion of cellulose."

The identification of acetic acid in the respirometer experiments suggests that this was the acid responsible for the odor observed by Randall and Doody. In order to check this a drop of .2 normal sulphuric acid was placed on a glass slide and the gut contents of 6 individuals of *Z. angusticollis* were squeezed out and immediately mixed with the drop of acid. A small watch glass was inverted over the acidified gut contents and its center kept cool by applying small pieces of filter paper saturated with cold water. The slide was heated first with a small flame and then with pieces of filter paper saturated with boiling water until the drop of gut contents had evaporated to dryness, the distillate being collected in the center of the watch glass. A minute bit of sodium uranyl carbonate was added to the distillate and it was placed in a covered dish to evaporate slowly. There were left the characteristic crystals of sodium uranyl acetate.

Bits of the wood used as food were tested for acetic acid in the same manner as above and so were fresh pellets. In neither case could any crystals of sodium uranyl acetate be detected. These data suggest that acetic acid is actually formed within the termite and is absorbed.

Experiment 10.

Cook ('32) noted that under anaerobic conditions there was a slow evolution of an undetermined gas (not carbon dioxide) in faunated but not in defaunated termites. Judging from the results of the above respirometer experiments in which hydrogen was identified as one of the products of a suspension of protozoa it seemed quite possible that this was the gas produced in the intact termite.

Termites from a laboratory colony of *Z. nevadensis* were studied under anaerobic conditions in 4 respirometer vessels all containing KOH and two provided with methylene blue-platinized asbestos. During 75 minutes there was a pressure increase of 8.7 mm. and 3.0 mm., respectively, in the vessels absorbing both carbon dioxide and hydrogen, whereas it was 16.6 mm. and 25.3 mm., respectively, in the vessels where only carbon dioxide was absorbed. Since the volume of the termites and absorbents in these experiments was small in comparison to the size of the vessel no great error is involved if the constant for hydrogen is used to convert the pressure changes into cubic millimeters. When this was done the gas production per gram of termites per hour was found to be 31 and 42, respectively, for the vessels in which only carbon dioxide was absorbed and 14 and 5, respectively, for the vessels containing both KOH and the hydrogen absorbent. This indicates that hydrogen production was in the neighborhood of 27 cubic millimeters per gram hour. This is of the same order of magnitude as was found in the experiments with a suspension of the gut contents (see below).

The difference between duplicate runs in the above experiment is rather large and in a number of other experiments a similar variation has been found. However, the gas production in vessels containing both hydrogen

and carbon dioxide absorbents has always been considerably less than in those where only carbon dioxide was absorbed. In experiments with defaunated termites a significant increase of pressure in an anaerobic vessel containing potassium hydroxide has never been observed. These results indicate that hydrogen is produced by the protozoa in the intact termite.

Experiment 11.

Cook ('32) noted that under anaerobic conditions more carbon dioxide was produced by defaunated than by faunated termites. This result would not be expected if the protozoa produce carbon dioxide as one of their metabolic products in the living termite. Several experiments using different laboratory colonies have been performed to test this anaerobic production of carbon dioxide and the results have been collected in table II. The figures in parentheses give the carbon dioxide production alone, the hydrogen production having been separately determined and subtracted from the total.

TABLE II. *Gas production under anaerobic conditions in cubic millimeters per gram of termites per hour*

	Faunated	Defaunated
Colony 1		
Experiment 1	165 ⁴	87
Experiment 2	205 ⁴	118
Colony 2	274 (233)	232
Colony 3		
Experiment 1	732 (518)	293
Experiment 2	849 (635)	232

⁴ The constant for carbon dioxide was used to calculate the amount of gas.

Since the hydrogen production has usually been found to be about one-fourth of the total gas production it would seem that more carbon dioxide was produced in the faunated termites of colony 1 than in the defaunated. In colony 2 there was no difference between them. Colony three shows a definite excess of carbon dioxide production in the faunated termites. This last colony is of interest because of the extremely large gas production. The gas exchange of 4 other individuals of this colony under aerobic conditions was studied and was found to show great differences from those previously observed and from those reported by Cook. The oxygen consumption was 364² cubic millimeters per gram of termites per hour whereas the gas production was 955 mm./gm. hr. In another later run the values of 406 and 785, respectively, were obtained.

The deviation of the respiratory exchange of colony 3 from the usual is most easily explained as due to a large production of gas by the protozoa.

² This figure has been corrected for hydrogen production as found in a separate experiment. It is lower than would be expected, possibly because of the large correction for hydrogen, this being determined from 4 other individuals whose production of this gas may have been lower than in the ones where oxygen absorption was studied. If this was the case the figure for gas production is also too low.

The fact that large amounts of hydrogen were found and that hydrogen is linked with the presence of the protozoa supports this explanation. It is significant that this was a small colony of *Z. angusticollis* in which there were many young present. In accordance with the hypothesis formulated at the beginning of this paper and as will be discussed later a respiratory exchange of the sort found is to be expected in the older nymphs of colonies containing a large proportion of dependent individuals. In the present connection, if the excess gas production of the faunated termites under anaerobic conditions be ascribed to the protozoa, it is quite clear that carbon dioxide is produced by them within the termite.

E. The magnitude of the anaerobic process

Since the data reported in the previous section indicate that in general the metabolic products of the protozoa within the termite are the same as those of suspensions in a suitable medium, and since where they can be estimated it appears that the amounts of the products under the two conditions are of approximately the same magnitude, it is possible to use the quantitative data obtained in experiments with suspensions to estimate the amounts of materials produced by the protozoa in the intact termite.

Using these amounts the question may be considered: Do the protozoa dissimilate anaerobically all of the sugars produced by digestion or is some of the sugar absorbed by the termite? In the table below are given the

TABLE III. *Summary of the amounts of metabolic products formed in a number of experiments, expressed as cubic millimeters per gram hour*

	Uncorrected termite O ₂ consumption	Acid production	Gas production	CO ₂ production	H ₂ production
<i>Z. nev.</i>	669	90	81 ^b		
<i>Z. nev.</i>		96	75 ^b		
<i>Z. ang.</i>	506	137	145 ^b		
	545	56	110 ^b		
	535		240	162	78
	535		155	103	52
					40
			155	128	27
			137	118	19
					70
		80			
		80			
Aver. for <i>Z. ang.</i>	524	88		128	48

^b These figures are a little too high because the vessel constant for carbon dioxide was used in converting the pressure change into cubic millimeters of gas.

amounts of acid, gas (when not analyzed for carbon dioxide and hydrogen components), carbon dioxide, and hydrogen produced in several different experiments. In some of these the oxygen consumption of the termites was also measured.

The figures for oxygen consumption were calculated from the pressure decrease in vessels containing termites and KOH. Since an amount of H_2 produced in the vessel would obscure the consumption of an equal amount of oxygen and since H_2 is evidently produced, the figure for the oxygen consumption is too low. Correcting it by the amount of hydrogen formed in the suspensions a figure of 572 cmm./gm. hr. is obtained.

The oxygen consumption of 572 cmm. per gm. hr. by *Z. angusticollis* indicates an average carbohydrate dissimilation of about 0.0044 millimols per gm. hr. (Hungate, '38). The acid production by the suspension of protozoa amounts to 0.004 millimols per gm. hr. The CO_2 production is 0.0057 millimols while the H_2 production is 0.0021 millimols per gm. hr.

The recovered products of the anaerobic dissimilation by the protozoa do not quantitatively account for all of the glucose assumed to be dissimilated. Of the .0264 millimols of carbon atoms present in the .0044 millimols of hexose, .0137 millimols are present in the acid and carbon dioxide produced, assuming that all of the acid was acetic acid. Of the .0264 millimols of O in the hexose .0194 millimols are recovered. Of the .0628 millimols of H .0202 millimols are recovered.

Neither do the recovered products represent qualitatively all the products formed in the dissimilation of the glucose. The relative proportions of carbon, hydrogen, and oxygen in the recovered products are about 2C : 3H : 3O. In glucose the proportions are 2C : 4H : 2O. Evidently hydrogen is present in the products in less and oxygen in greater proportion than in the original substrate. Other products containing relatively more hydrogen and less oxygen must have been formed during the dissimilation process. Tests for lactic acid, pyruvic acid, acetaldehyde, glucose, and methyl glyoxal have failed to demonstrate these materials in any significant amount. A single preliminary test for glycerine, and two for ethyl alcohol have also been negative.

Although some of the products of the anaerobic carbohydrate metabolism of the protozoa have not as yet been identified the recovered carbon accounts for about one-half of the carbohydrate dissimilated in the termite. When the other as yet undetermined products are also taken into account it appears quite possible that most of the hexose formed as a product of digestion by the protozoa undergoes an anaerobic dissimilation by them.

DISCUSSION

Use of data on oxygen consumption to calculate the amount of polysaccharide digested in the termite is open to the criticism that during the short intervals in which measurements were made the protozoa may have been digesting more cellulose than was being used in the combined metabolism of the termite and the protozoa. The importance of chance variations is decreased to some extent by the fact that a number of separate determinations were made and the average value used. However, it is well known that the members of a termite colony are not all equally capable of obtaining food.

The soldiers, reproductive individuals, and very young nymphs are fed by the remainder of the colony, the older nymphs. Since nymphs of the later instars were used in all the above experiments they probably digested an amount of wood in excess of the amount needed to satisfy their own energy requirements. The additional materials were perhaps used in growth, were stored as reserve carbohydrates, or were fed to other members of the colony. Thus, the figure of .0044 millimols as the amount of glucose available is possibly too low.

Several considerations indicate that the digested glucose over and above the amount needed to satisfy the immediate energy requirements is not very great. The increase in dry weight of a group of termites has been found in one experiment to be only about one-tenth of the weight of the materials oxidized (Hungate, '38). The digestion of this proportion of material for growth and (or) storage of reserve carbohydrates would only increase the figure of .0044 millimols to .0048.

The question as to how much excess wood must be digested in order to feed other members of the colony may be estimated in a very approximate fashion. The weight of the termites capable of wood digestion in a colony is probably greater than that of the individuals dependent upon them for food. Goetsch ('36) has observed that the ratio between workers and soldiers in colonies of *Kaloterмес* is usually 15–20 to 1. This approximate ratio has also been noted between soldier nymphs and soldiers in *Zootermopsis*. The reproductive members of a colony are also usually much fewer in numbers than the wood-eating nymphs. The dependent young, while often numerous, are not as large as the nymphs feeding them so that on the basis of weight and energy requirements they also probably constitute only a small part of the colony. While occasional exceptions may be noted (as in experiment 11) it seems probable that the amount of digestion over and above that necessary to satisfy the energy requirements of the termites and protozoa in which the digestion occurs is not very great, possibly not more than fifty per cent larger than the amount needed to satisfy the immediate energy requirements of the individuals used.

If this excess glucose is dissimilated by the protozoa then the products recovered should be compared to a number larger than the .0044 millimols of glucose/gm. hr. calculated to be formed by digestion. It should also be pointed out, however, that the method of removing the protozoa from the hind-gut by squeezing the abdomen of the termite did not remove all of the protozoa from the gut. This deficiency would tend to counteract a capacity of the protozoa to digest and metabolize more carbohydrate than was completely oxidized in the combined metabolism of the termite and the protozoa. Furthermore, in all suspension experiments the amounts of metabolic products formed by the protozoa gradually fell off, so that if the amounts they at first formed in the suspension be supposed to be indicative of their activity in the termite the figures obtained are somewhat low.

From quite other considerations the dissimilation of most of the glucose by the protozoa in the intact termite is suggested. Their anaerobic nature seems fully established. They must have a source of energy. The experiments of Cook ('32) on the gas exchange of faunated and defaunated termites suggest that the protozoa have an energy requirement about one-eighth that of the termite. Although this figure can only be considered as a rough approximation the data do suggest that the energy requirements of the protozoa are not negligible as compared to those of the termite itself.

That they are not negligible also follows from the fact that the weight of the protozoa constitutes an appreciable part of the weight of the termite-protozoa complex. In one experiment 4.8 gm. of *Z. angusticollis* were used to obtain protozoa by squeezing the abdomen. Any pellet or material in the posterior part of the gut which seemed to be principally wood was placed on a watch glass and these accumulated pellets were weighed as were also the termites after removal of the protozoa. The weight of the termites was 3.90 gm. while the pellets amounted to .113 gm. Evaporation of water from the pellets could not be entirely prevented during the removal of the protozoa and pellets from remaining termites so the value for the weight of the pellets is too low. If it be estimated at about .2 to .3 gm. then the weight of the gut contents containing the protozoa was .7 to .8 gm. This constitutes one-sixth to one-seventh of the weight of the faunated termite. In another experiment the weight of the gut contents was one-fourth of the total. Although much of the gut contents is water and wood particles the protozoa make up a considerable part of it. When the undiluted gut contents were centrifuged in an air driven ultra-centrifuge (Hungate, '36) the supernatant fluid was found to be only about one-half of the total. It is also easily seen under the microscope that the bodies of the protozoa make up a large part of the gut contents of *Zootermopsis*.

These protozoa are extremely active and must have a high energy requirement. Since they are anaerobic and since the amount of energy obtainable from an anaerobic process is relatively small it would seem that they must use large quantities of substrate in order to meet their energy requirements.

Although it is evident that there are difficulties involved in estimating the amount of glucose formed by digestion in the above experiments still the amount of metabolic products recovered and the fact that most other considerations point toward the utilization of large quantities of substrate by the protozoa make it highly probable that most of the glucose formed in digestion is further dissimilated. Failure of the author and of Trager ('34) to find glucose in suspensions of the protozoa is further support for this conclusion.

CONCLUSIONS

The protozoa in *Zootermopsis* are anaerobic. When they are mechanically separated from the termite and suspended in suitable media their metabolic products accumulate in sufficient quantity to be identifiable and meas-

urable. Carbon dioxide, hydrogen, and acetic acid have been identified as metabolic products of the protozoa. Other unidentified products are also formed. The metabolism of the protozoa within the termite appears to be the same as that when they are removed and suspended in a suitable medium.

The metabolic products recovered are sufficient in quantity to indicate that most of the glucose formed by the protozoa in digesting cellulose and hemicellulose is metabolized by the protozoa.

With the data thus far accumulated a further insight into the intimate symbiotic relationship of the termite and its protozoa is obtained. The two groups are associated in a mutually beneficial decomposition of the carbohydrates of wood in which the following factors may be postulated: (1) the termite comminutes the wood and transports it to the hind-gut where (2) the protozoa digest it and (3) metabolize it anaerobically, thereby deriving their necessary energy and forming metabolic products which (4) are absorbed by the termite and oxidized to satisfy its energy requirements, an action which not only serves the termite but also aids the protozoa by (5) removing harmful metabolic products. In addition, the oxygen needs of the termite maintain a low oxygen tension which (6) permits the protozoa to survive and at the same time insures that their metabolism shall be anaerobic and result in products useful to the termite.

The unique conditions which the protozoa require and which the termite supplies may explain in part the restricted distribution of the protozoa.

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EFFECTS OF FREQUENT CLIPPING ON THE UNDERGROUND FOOD RESERVES OF CERTAIN PRAIRIE GRASSES¹

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A series of experiments in which true-prairie grasses were clipped at frequent intervals afforded excellent materials for a study of the effects of such treatment upon the food reserves. Two species of *Andropogon*, at present the most important dominants of true prairie, were employed. A series of quadrats on a north-facing slope in the Belmont prairie at Lincoln, Nebraska, in which little bluestem, *Andropogon scoparius*, grew in about 70 per cent pure stand, was the source of one lot of underground parts. Those of big bluestem, *A. furcatus*, were obtained about a mile distant from virgin lowland prairie near the flood plain of Salt Creek.

Permanent quadrats were marked out in the spring of 1933. The grasses in some were used for controls; in others they were cut close to the ground (in this manner simulating very closely grazed pastures) six times during the growing season, *viz.* May 9 and 27, June 25, July 27, August 27, and October 10. During the drought year of 1934 the grasses were clipped only four times, May 15, June 13, July 22, and September 27. Only two clippings were made during 1935, due to a dry spring and extreme drought after midsummer. Control quadrats were clipped once each year in October. The last samples were collected on July 25, 1935, after vegetative growth was completed.

Samples consisted of the bases of the culms of the little bluestem occurring below ground and the roots to a depth of 10 centimeters. Big bluestem has, in addition, pronounced shallow rhizomes, which were also taken to the 10-centimeter depth. At each sampling materials were secured from both clipped and control quadrats. These were freed from all soil and other foreign matter and then rapidly air dried. After the first year, especially, the samples from the clipped quadrats represented not the average of the whole quadrat but rather the average of the remaining living plants. For example, one-fourth square meter of a control quadrat furnished an abundance of materials from which the samples for chemical analyses could be taken. A sample from the clipped quadrats required much more area—finally over a square meter to secure adequate materials. Although many plants had died, roots and rhizomes were not taken from these, at least not in quantity, since they were often too fragile to withstand the severe brushing necessary thor-

¹ Contribution no. 111 from the Department of Botany, University of Nebraska.

oughly to cleanse them from soil. Moreover, the species could not always be identified with certainty from these dead remains.

The grasses were in a vigorous condition before the experiment was begun, since both tracts were virgin, unpastured prairie, and rainfall had been adequate for an excellent growth. They had been mowed annually in the fall for the crop of hay.

The initial sampling was done on April 4, 1934, after one year of close clipping, and before growth had been renewed. The second lot of samples was dug on June 16, three days after the second seasonal clipping. Grasses in the control upland plots were 9 inches tall and those in the lowland 12 inches. A third sampling was made in the clipped plots in October, after the plants had completed growth. In 1935, samples were secured from both clipped plots and controls, after the grasses in the latter had completed growth late in July.

The purpose of the chemical study was to make such determinations as would give direct information on the amount of stored food materials. It was believed that the loss in organic materials would increase the percentage of ash, due to a decrease in weight of the organic food materials while the inorganic portion remained constant. Hence, determinations of the total ash and insoluble ash were made. Determinations were also made of the invert sugar, the water-soluble hydrolyzable materials, water-insoluble hydrolyzable materials, pentosans, and nitrogen. They all have a direct bearing on the stored materials which are essential to continued growth of the plants.

Samples for analysis were obtained by grinding the air-dried underground stems and roots in a Wiley mill, using a .5 mm. screen. The finely ground material was then placed in a pebble mill and reduced to a very fine powder. It was thought that the latter treatment might increase the silica content of the ash. However, results obtained from material directly from the Wiley mill were compared with those obtained from the pebble mill. They showed that the loss of silica from the pebble mill was negligible. Materials were pulverized in order to insure complete extraction for the carbohydrate determinations. Three samples were used in each assay in order to assure comparable results. In nearly all cases there was close agreement among the triplicate samples. Averages of the determination were employed.

METHODS OF ANALYSIS

The methods of analysis used in these procedures will be stated only briefly since the exact methods may be found in the "Methods of Analysis," published by the Association of Official Agricultural Chemists.

The determination of ash was made by burning at a low temperature (550° C., dull redness) a desired sample of the dry powdered material until a white ash of constant weight was obtained.

The acid insoluble ash was determined from the ash samples by heating with hydrochloric acid (dilution 1 to 2.5) for 5 minutes, then transferring

to a tared Gooch crucible, washing with water, and then igniting to a constant weight.

The determination of the invert sugar was made by using 10 gm. of the air-dried material. This was placed in a 250 cc. volumetric flask, 150 cc. of alcohol (50 per cent by volume) were added and the mixture heated on a water bath for one hour. The flask was removed from the water bath after heating and allowed to stand over night. It was next made up to the 250 cc. mark with 95 per cent alcohol, filtered, and 200 cc. of the filtrate evaporated to about 20 cc. This was placed in a 100 cc. volumetric flask and cleared with lead acetate and sodium carbonate. A sample of 25 cc. of this filtrate was used for a determination by the Munson and Walker method for invert sugar.

The water-soluble hydrolyzable material was determined by using a 50 cc. sample of the above filtrate. This was neutralized with acetic acid after which 5 cc. of hydrochloric acid were added and the mixture allowed to stand 24 hours for hydrolysis. The solution was then neutralized with sodium carbonate, 50 cc. of this solution were used for a Munson and Walker determination of the total invert sugar.

The water-insoluble hydrolyzable material was determined by using 2.5 gm. of the material which was mixed with 50 cc. of water and allowed to stand for 1 hour. This was then placed in a filter and washed with 250 cc. of cold water to remove the soluble portion. The insoluble residue was transferred to a 250 cc. volumetric flask to which 200 cc. of water and 20 cc. of hydrochloric acid (dilution 5 to 4) were added and the mixture refluxed for 2.5 hours. After neutralizing and clearing, a determination of the reducing value after hydrolysis was made by using the Munson and Walker method. The results were reported as invert sugar.

The determination of nitrogen was made by using the Kjeldahl method with Gunning's modification.

The pentosans were determined by distilling a desired quantity of the ground material with dilute hydrochloric acid. The distillate, which measured 350 cc., was precipitated with phloroglucin. This precipitate was collected in a tared Gooch crucible, thoroughly washed, dried to constant weight, and from this value, using the designated factor, the weight of apparent pentosans was calculated.

RESULTS

The total ash and acid insoluble ash of the roots and underground stems are given in table I.

An inspection of the table shows that the proportional increase in percentage of ash due to the loss in organic material, which was expected, did not occur. In fact, there does not seem to be any constant trend in increasing or decreasing quantities of ash. This may be due to the tiny particles of soil which adhered so tightly to the roots and rhizomes that it was im-

possible to remove them. It should be pointed out, however, that the samples used were free from all visible soil particles. The individual analyses in most cases varied not more than .05 per cent which indicated that the material was of uniform composition.

TABLE I. *Percentage of total ash and acid insoluble ash of roots and underground stems of Andropogon furcatus (Af) and A. scoparius (As) in the surface four inches of soil*

Time of sampling	Roots of Af		Rhizomes of Af		Roots of As		Stem bases of As	
	Control	Clipped	Control	Clipped	Control	Clipped	Control	Clipped
A. Total ash								
April 4, 1934	7.23	8.97	8.25	6.51	8.34	7.25	5.98	8.64
June 16, 1934	6.14	7.63	5.91	8.92	5.87	6.69	8.12	6.87
Oct. 15, 1934	—	8.86	—	6.36	—	5.71	—	4.45
July 25, 1935	6.80	7.48	5.92	6.46	6.48	6.36	4.39	6.80
B. Acid insoluble ash								
April 4, 1934	6.18	7.59	6.65	5.57	7.19	6.59	4.75	7.55
June 16, 1934	5.19	7.43	5.03	6.50	4.63	6.14	7.32	6.13
Oct. 15, 1934	—	7.08	—	4.38	—	4.98	—	3.58
July 25, 1935	6.43	6.27	4.90	4.79	5.56	5.46	3.87	5.06

The invert sugar, the water-soluble materials, and the water-insoluble materials capable of reduction of the cupric ion after hydrolysis are shown in table II. From these data, one is able to obtain some idea of the relative proportion of the food distribution in these grasses.

The small amount of invert sugar represented by the samples collected in April may be accounted for by the fact that although the grasses had not broken dormancy, a few swollen buds were observed while washing the rhizomes. It is also obvious that the percentage was less for the clipped than the control samples, with the exception of the stem bases of little bluestem. These results were obtained from the material after one year of clipping. The second lot of samples, from the control and clipped areas on June 16, 1934, showed in every case a lower percentage of invert sugar in the clipped than in the control samples, although the total percentages were much higher than earlier in the season. In October, after the plants had completed their growth, the results were more nearly comparable to the values obtained in April of the same year. The difference between the results of June and October are to be expected, since there are more soluble nutrients in a growing plant than in one that is dormant.

In 1935, the samples were collected after the plants had completed their

TABLE II. Percentages of invert sugar, the water-soluble hydrolyzable material and water-insoluble hydrolyzable material expressed as invert sugar for the roots and underground stems of *Andropogon furcatus* (Af) and *A. scoparius* (As) in the surface four inches of the soil

Time of sampling	Roots of Af		Rhizomes of Af		Roots of As		Stem bases of As	
	Control	Clipped	Control	Clipped	Control	Clipped	Control	Clipped
A. Invert sugar								
April 4, 1934	.46	.27	.46	.05	.63	.15	.40	.59
June 16, 1934	1.67	1.00	1.34	1.08	1.94	1.16	2.88	1.45
Oct. 15, 1934	—	.13	—	.20	—	.25	—	.08
July 25, 1935	1.33	1.23	.75	.39	1.39	.70	1.37	.15
B. Water-soluble hydrolyzable material as invert sugar								
April 4, 1934	3.13	1.21	4.08	3.47	3.85	3.21	5.22	2.71
June 16, 1934	1.97	2.01	1.78	1.44	2.35	1.45	.98	.63
Oct. 15, 1934	—	2.12	—	1.80	—	1.24	—	1.31
July 25, 1935	1.27	1.06	1.12	.46	1.81	.74	1.48	.66
C. Water-insoluble hydrolyzable material as invert sugar								
April 4, 1934	27.39	14.79	31.93	25.15	28.11	25.84	27.99	27.73
June 16, 1934	26.50	25.95	27.23	27.48	27.98	27.70	29.24	30.94
Oct. 15, 1934	—	17.53	—	18.70	—	16.12	—	13.78
July 25, 1935	21.45	20.72	14.68	18.49	24.21	9.36	21.08	13.97

vegetative growth. The controls gave much lower values than in June, 1934. This probably resulted from the very dry spring. Comparison of the controls with the clipped samples of July, 1935, shows a very decided decrease in the percentage of invert sugar. A comparison of both the control and the clipped samples for 1934 and 1935 shows the effect of severe clipping over a period of three years upon the food reserves in the form of soluble invert sugars. In big bluestem the amount in the roots of both control and clipped plants usually greatly exceeded that of the rhizomes. In little bluestem, where the stem bases are much more limited storage organs, this relationship did not hold. The low percentage for the clipped samples in 1935 corresponded with the lowered vitality of the plants, and the death of many of them.

A study of parts B and C of table II shows that the clipped grasses without exception, had less water-soluble hydrolyzable material and water-insoluble hydrolyzable material on April 4, 1934, than their controls. A decrease in percentage of food materials for both the clipped and control grasses was noted, however, as in A, from 1934 to 1935.

Table III is divided into two parts, A, the percentage of pentosans as

calculated from the furfural produced in the experiments, and B, the percentage of nitrogen.

TABLE III. *Pentosans and nitrogen of roots and underground stems of Andropogon furcatus (Af) and A. scoparius (As) in the surface four inches of soil*

Time of sampling	Roots of Af		Rhizomes of Af		Roots of As		Stem bases of As	
	Control	Clipped	Control	Clipped	Control	Clipped	Control	Clipped
A. Pentosans								
April 4, 1934	17.08	21.30	24.38	15.68	18.36	14.78	22.71	25.74
June 16, 1934	21.92	23.52	24.72	23.93	24.68	24.36	30.19	26.86
Oct. 15, 1934	—	19.83	—	22.46	—	21.13	—	26.80
July 25, 1935	20.68	10.08	22.52	24.19	9.09	22.71	23.71	24.71
B. Nitrogen								
April 4, 1934	.68	.75	.76	.72	.77	.66	.76	.69
June 16, 1934	.58	.51	.46	.61	.42	.47	.48	.51
Oct. 15, 1934	—	.59	—	.73	—	.60	—	.61
July 25, 1935	.60	.46	.73	.75	.72	.78	.74	.75

This portion of the study gave a series of very erratic results from which it would be difficult to draw any conclusions. It may be noticed that there was less change in the percentage of pentosan in the rhizomes and stem bases than in the roots, although the values remained relatively constant over the two-year period. This may be due to the abundance of bract-like appendages over the surface of these stems which under the conditions of the experiment would no doubt yield quantities of furfural. The roots, being of different structure, would yield a smaller amount of furfural and would, therefore, have a lower percentage.

As nearly constant results were obtained in determinations of nitrogen as might be expected from plant material of this type. The results show almost a constant nitrogen balance even under adverse conditions of growth. It may be noticed that the lowest percentages were found in the samples of June 16, of the extremely dry year 1934.

CONCLUSIONS

The percentage of ash and acid insoluble ash gave no insight into the quantity of food reserves of the plant.

The ash content varied between 4.4 and 9 per cent and the acid insoluble ash between 3.6 and 7.6 per cent.

There was a marked decrease in the percentage of invert sugar, water-

soluble hydrolyzable material and water-insoluble hydrolyzable material under conditions of severe clipping.

Drought during 1934 and 1935 had a similar but smaller effect on the stored nutrients of the control plants for comparable periods (June and July).

The pentosan determination, owing to the formation of furfural from stem parts, proved of little value in the determination of nutrients.

The percentage of nitrogen was almost constant, varying approximately between .42 and .78 per cent under all the conditions of growth studied.

Severe clipping of *Andropogon scoparius* and *A. furcatus* decreases the amount of foods stored by the plants in their roots, thus resulting in their destruction in a period of a few years.

THE OXYGEN THRESHOLD FOR THREE SPECIES OF FISH¹

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The purpose of this investigation was to determine the oxygen threshold for three species of fish. Much work has been done in this field on various species of fish and by numerous methods; the results, however, vary widely. Kupzis ('01) states that the European roach (*Leuciscus erythrophthalmus*) can live for sometime in water containing 1.0 p.p.m. dissolved oxygen, but it cannot exist in a concentration below 0.57–0.71 p.p.m. Plehn ('24) reports that trout live best in water containing 10.0–11.43 p.p.m., and if the water is warm, they show signs of distress at 7.86 p.p.m. He also states that a concentration of 7.1 p.p.m. is sufficient for carp and that these fish show signs of distress when the concentration is below 4.3 p.p.m. In cold water, the carp can live for a short time at a concentration of 0.71 p.p.m. Gardiner and King ('22) found that the asphyxial point for trout was 1.14 p.p.m. at 6.5° C. and 3.4 p.p.m. at 25° C. The minimum concentration for goldfish was found to be 0.56 p.p.m. at 11° C. and 0.6 p.p.m. at 27° C. Paton ('04) reports that 2.9 p.p.m. of dissolved oxygen is the threshold for young trout. Gutsell ('29) showed that brown and rainbow trout were asphyxiated in an oxygen content of 2.5 p.p.m. at 10° C. Ellis ('37) states that 3.0 p.p.m. at 25° C. is the upper limit of dissolved oxygen at which asphyxia may be expected for most fresh water fishes.

Some of the factors that influence a problem of this type are temperature, hydrogen ion concentration, dissolved carbon dioxide, organic and inorganic toxic materials, and the size and species of fish. Starvation or heavy feeding may be factors. The methods used in these experiments attempted to control as many factors as possible in order that the results would depend only upon the amount of dissolved oxygen present. The fish used were the yellow perch (*Perca flavescens* Mit.), the steel-colored shiner (*Notropis whipplii* Gir.), and the blunt-nosed minnow (*Hyborhynchus notatus* Raf.).

¹ The writer is indebted to the late Professor Will Scott and to Dr. W. R. Breneman for their many useful suggestions in this work and to the other members of the Zoology Department of Indiana University who gave him helpful criticisms and advice. The writer is also indebted to the Indiana Conservation Department for financial assistance during part of this investigation.

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METHODS

Two methods were used. In the first method, fish were placed in battery jars containing two liters of water, and the supply of oxygen was reduced by their respiration. The surface of the water was covered with a floating screen, making it impossible for the fish to gulp air. At the beginning of each experiment, the temperature was taken and an analysis was made of the oxygen and hydrogen ion concentration. Dissolved oxygen was determined by the Winkler method as outlined in the seventh edition of *Standard Methods of Water Analysis*, published by the American Public Health Association. The hydrogen ion concentration was measured with the Hellige Wide Range Indicator. A control jar of water was also analyzed at the beginning and termination of each experiment. When one or more of the fish showed symptoms of asphyxiation, as manifested by rapid opercular movements, loss of balance, and irregular motions, the water was again analyzed, and the size, weight, and number of the fish were recorded. Belding ('29) showed that fish in a toxic environment had a high respiratory rate as determined by the opercular movements. Although no respiratory counts were made, an increased opercular rate was noticed when the oxygen content was low. Observations showed that when one fish was asphyxiated, the remaining fish showed signs of oxygen deficiency.

The second method of determining the oxygen threshold was by the use of running water having a low oxygen concentration. Fish were placed in flasks of 1200 cc. and 250 cc. capacities containing tap water. This water flowed through the flask for one to three hours. Then water containing a small amount of oxygen was run through the flasks, at the rate of three liters per hour, gradually replacing the tap water. The rate of flow fluctuated slightly according to the water level of the supply tank.

The amount of oxygen in the water was decreased by boiling the water for one hour and cooling it in metal condensers. This water was allowed to flow over the fish until one or more of them showed signs of asphyxia. At that time, the oxygen, temperature, and pH were measured. The system was air-tight, so that the fish were unable to gulp air. All of the analyses were made of water taken from the flasks containing fish.

When water is boiled, some of the carbonates and free carbon dioxide are removed, thus changing the pH of the water. In these experiments the pH was changed from 7.0 to between 8.0 and 8.8. In eleven experiments on yellow perch, sulfuric acid was added to neutralize the water. No toxic effects were noted. This acid was used because, according to the results of Ellis ('34), the sulfate radical appears to be the least toxic of the anions in available acids. Powers ('22) shows that marine fishes are able to extract oxygen from water equally well through a wide range of hydrogen ion concentration, and ('30) he presented a critical review of the subject concerning the relationship between aquatic animals and the hydrogen ion concentration.

YELLOW PERCH

Considerable variation exists in the literature regarding the oxygen threshold for the yellow perch. The results of Smith ('25) show that the perch does not tolerate an oxygen content below 2.35 p.p.m. for more than four hours. He lowered the fish in wire baskets to a depth of 45 to 50 feet in Douglas Lake, Michigan, and noted their survival time in reference to the dissolved oxygen. Some variation is present in his results which may be due to other conditions of the water at that depth. These data differ from those of Pearse and Achtenberg ('20), who state that the yellow perch can live for two hours in water containing 0.3 p.p.m. of oxygen, although the majority of their fish turned over within a few minutes. Wiebe *et al.* ('34) placed the perch in closed jars of water and the analyses were made when all of the fish were dead. His results showed that perch were able to extract oxygen to slightly less than 0.5 p.p.m., at a temperature of 25° C. and pH of between

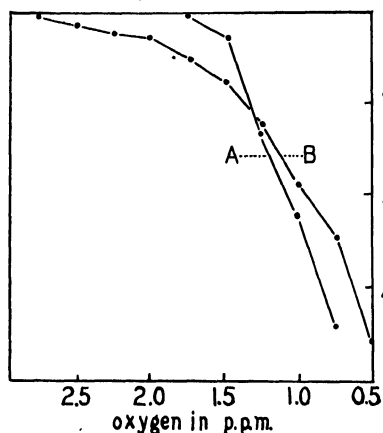


FIG. 1

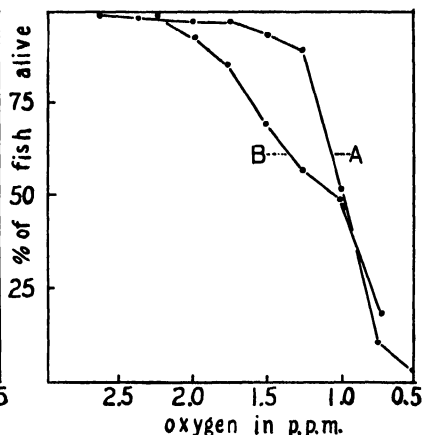


FIG. 2

FIG. 1. Low oxygen experiments using yellow perch. A. Battery jar method, tap and lake water used. B. Running water used, low in oxygen.

FIG. 2. Low oxygen experiments using the steel-colored shiner. A. Battery jar method. B. Running water used, low in oxygen.

4.5 and 9.0. In my own experiments, the final analyses of oxygen, pH, and temperature were made when one or more of the fish in a jar showed evident signs of asphyxia. They were alive even though suffering from a lack of oxygen.

The results of the battery jar method, when yellow perch were used, are presented in figure 1 and table I. The ordinate of figure 1 represents the percentage of the total number of fish alive at the oxygen concentration shown by the mantissa. Thirty-three fish were used in 23 battery jars. The average duration was seven and one-half hours; the pH ranged from 7.0 to 7.8,

TABLE I. *Results of 23 battery jar and 36 running water experiments using 93 yellow perch, average length 76.5 mm., average weight 5.52 grams*

Asphyxial oxygen in p.p.m.	Battery jar method pH 7.0-7.8 temp. 18°-25° C. average duration 7.5 hrs.		Running water method pH 8.3-9.1 temp. 20°-27° C. average duration 1.0 hr.	
	No. fish alive	No. fish asphyxiated	No. fish alive	No. fish asphyxiated
0.0-0.50	—	—	0	4
0.51-0.75	—	—	7	19
0.76-1.00	6	6	5	6
1.01-1.25	4	2	5	7
1.26-1.50	6	2	7	3
1.51-1.75	7	2	7	0
1.76-2.00	33	0	4	0
2.01-2.25	—	—	5	0
2.26-2.50	—	—	1	2
2.51-2.75	—	—	—	—
2.76-3.00	—	—	2	1
3.25-3.50	—	—	60	0

and the temperature from 18° to 25° C. The variation of the pH and temperature had no noticeable effect upon the asphyxial point of the fish. None of the fish were asphyxiated in an oxygen concentration of 1.75 p.p.m., 93 per cent were alive in a concentration of 1.50 p.p.m., 50 per cent alive in 1.07 p.p.m., but only 15 per cent were alive in 0.75 p.p.m.

Water low in oxygen was also run through air-tight flasks containing fish, as a check on the asphyxial point found by the battery jar method. This method, as previously described, eliminated any possible toxic effects of the waste products, but it introduced the factor of high alkalinity. The results obtained from 33 experiments on 60 yellow perch, using this method, are plotted in figure 1 and table I. Thirty-seven of these fish were used in highly alkaline water of between pH 8.6 and 9.1, and the remaining twenty-three fish were used in water in which the pH was reduced with sulfuric acid. The average time of these experiments was one hour and two minutes. The oxygen concentrations at the time of asphyxia were similar in each case and are plotted on the same curve. The recorded data show that the temperature variation of from 20° to 27° C. had no apparent effect upon the asphyxial oxygen value.

The curve (Fig. 1) indicates that there is wide individual variation among fish of the same species when they are subjected to similar experimental conditions. The asphyxial amount of oxygen ranged from 2.75 to 0.5 p.p.m. with the sharpest drop occurring when the oxygen value was 1.75 p.p.m. Only 70 per cent of the fish were alive in an oxygen concentration of 1.25 p.p.m., and 93 per cent of the fish were apparently in good condition in a concentration of 2.00 p.p.m.; therefore, the minimum toleration point, under these conditions, must be greater than 2.00 p.p.m. The oxygen threshold found by this method is slightly higher than the value determined by the

battery jar method. The average length of the fish was 76.5 mm. and the average weight 5.52 grams.

Many of the fish were revived in fresh water after they had been asphyxiated to the stage of loss of balance. This reaction is contrary to the results of Hubbs ('30) who showed that, when nascent oxygen was used, the fish could not be revived.

STEEL-COLORED SHINER

The results of 25 experiments on the steel-colored shiner, using the battery jar method, are shown in figure 2 and table II. The range in pH was

TABLE II. *Results of 25 battery jar and 12 running water experiments using 102 steel-colored shiners, average length 51.2 mm., average weight 3.77 grams*

Asphyxial oxygen in p.p.m.	Battery jar method pH 6.8-7.0 temp. 20°-25° C. average duration 15.7 hrs.		Running water method pH 7.7-9.2 temp. 22°-24° C. average duration 1.02 hrs.	
	No. fish alive	No. fish asphyxiated	No. fish alive	No. fish asphyxiated
0.0 -0.50	0	2	—	—
0.51-0.75	3	2	—	—
0.76-1.00	8	11	6	3
1.01-1.25	13	22	8	1
1.26-1.50	19	5	1	2
1.51-1.75	0	1	2	1
1.76-2.00	2	1	33	0
2.01-2.25	69	0	—	—

from 6.8 to 7.0, and the temperature varied from 20.5° to 25.0° C. This difference, as in the preceding experiments, showed no effect upon the asphyxial point. A total of 69 fish was used having an average length of 51.2 mm. and an average weight of 3.77 grams. The water in all of the jars except five was covered with a floating screen. In the five open jars, the fish survived for about 25 hours, and in the screened jars, the average time was about 9 hours. The amount of oxygen present at the time of asphyxia was, within the limits of experimental error, the same in both cases.

The data show that no fish suffered from lack of oxygen above a concentration of 2.60 p.p.m., 90 per cent were alive at 1.25 p.p.m., 53 per cent were alive at 1.00 p.p.m., and all succumbed at less than 0.75 p.p.m. The curve (Fig. 1) shows that when the oxygen level was reduced to 1.50 p.p.m., the asphyxiation rate of the fish increased rapidly. The results of Wiebe *et al.* ('34) show that under similar conditions, the steel-colored shiner (*Erogala whippelii* Gir.) is able to reduce the oxygen to slightly less than 1.00 p.p.m. However, his fish were dead when the analyses were made; therefore, that oxygen concentration cannot be considered as the oxygen threshold.

The results of twelve experiments using running water low in oxygen upon 33 steel-colored shiners are plotted in figure 2 and table II. The temperature range of these experiments was from 22° to 24° C. and the pH

range from 7.7 to 9.2. The average length of the shiners was 52.3 mm., the average weight 3.97 grams, and the average duration of the experiments was 61 minutes. The results show that none of the fish suffered from a lack of oxygen when the concentration was 2.25 p.p.m. or higher, 92 per cent were alive at 2.00 p.p.m., 57 per cent were alive at 1.25 p.p.m., and none of the fish survived in less than 1.00 p.p.m. of oxygen.

The results of the two series of experiments on the steel-colored shiners show that 97 per cent of the fish used in the battery jars and 92 per cent of the fish used in the running water were in good condition in an oxygen concentration of 2.00 p.p.m. when the temperature ranged from 20.5° to 25.0° C. and the pH from 6.8 to 9.2. When the oxygen was reduced below 2.00 p.p.m. by either of the above methods, the number of fish asphyxiated increased rapidly. Under these experimental conditions, therefore, the oxygen threshold for this fish must be considered above that figure, or approximately 2.25 p.p.m.

BLUNT-NOSED MINNOW

A series of battery jar experiments were run using 165 blunt-nosed minnows. The average length of the fish was 40.9 mm. and the average weight was 0.90 grams. The temperature ranged from 20.5° to 24.0° C. and the pH from 6.8 to 7.0. The carbon dioxide concentration was measured at the beginning of each experiment and again when the fish showed evidence of asphyxiation. The amount of carbon dioxide was determined by titration against sodium hydroxide. The range of the carbon dioxide at the asphyxial point was from 10.0 to 18.0 p.p.m. Recorded data show that there was no correlation between the concentration of the carbon dioxide and the oxygen-asphyxiation point. The average time for each experiment was ten and one-half hours.

The results (figure 3 and table III) show a wide individual variation for the species when they are under similar conditions. The asphyxial oxygen concentration varied from 2.75 to 0.75 p.p.m. The data recorded show that some of the fish were asphyxiated in a relatively high oxygen content. It is possible that these fish died because of injuries incurred during handling, as they were caught the day before they were used. In all of the other experiments, the fish were kept in out-door ponds for at least one week. If 10 per cent of the fish died because of injuries, then the curve shows the oxygen threshold to be approximately 2.25 p.p.m.

Two experiments were made using a total of 87 blunt-nosed minnows to determine the effect of temperature upon the ability of the fish to extract oxygen. The battery jar method was used and the temperature was lowered to between 7° and 12° C. The asphyxial oxygen concentration in these experiments was 1.75 p.p.m. There were 92 per cent of the fish alive at 1.5 p.p.m., 72 per cent at 1.00 p.p.m., and 35 per cent at 0.75 p.p.m. The average duration of the experiments was 179 hours. This was approximately 15 times

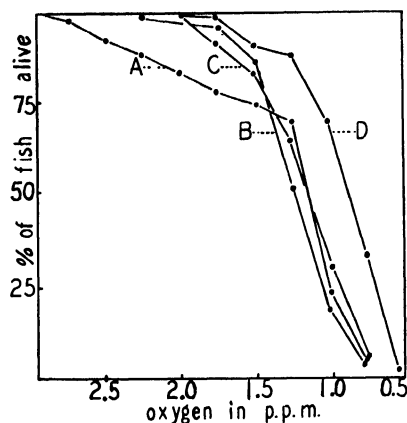


FIG. 3. Low oxygen experiments using the blunt-nosed minnow. A. Battery jar method, tap water used, temp. 20.5°–24° C. B. Battery jar method, boiled and aeriated water used. C. Running water used, low in oxygen. D. Battery jar method, tap water used, temp. 7°–12° C.

TABLE III. Results of 39 battery jar experiments using 252 blunt-nosed minnows in tap water at different temperatures

Asphyxial oxygen in p.p.m.	Temp. 20.5°–24.0° C. pH 6.8–7.0 final CO ₂ 13.3 p.p.m. average duration 10.5 hrs.		Temp. 7°–12° C. pH 7.0 final CO ₂ 16.8 p.p.m. average duration 179 hrs.	
	No. fish alive	No. fish asphyxiated	No. fish alive	No. fish asphyxiated
0.51–0.75	—	—	5	5
0.76–1.00	15	7	46	30
1.01–1.25	28	54	34	14
1.26–1.50	36	8	15	5
1.51–1.75	3	2	—	—
1.76–2.00	5	3	15	1
2.01–2.25	9	7	87	0
2.26–2.50	1	3	—	—
2.51–2.75	6	6	—	—
2.76–3.00	2	2	—	—
3.25–3.50	165	0	—	—

greater than the average duration of previous experiments at a higher temperature. The average length of the fish was 32.9 mm. and the average weight 0.61 grams.

An improved apparatus (Fig. 4) was built to use in experiments requiring water low in oxygen. An 18-gallon, iron tank replaced the 12-gallon, copper one used in the previous experiments, and a cylinder of nitrogen with a needle valve was used to control the oxygen concentration of the water. In order to obtain water as free as possible from oxygen, tap water was run in the tank and heated to the boiling point; and to exclude air, nitrogen gas under a pressure of 2.5 pounds was turned into the top of the tank. This procedure reduced the oxygen content to about 0.5 p.p.m., but with the ad-

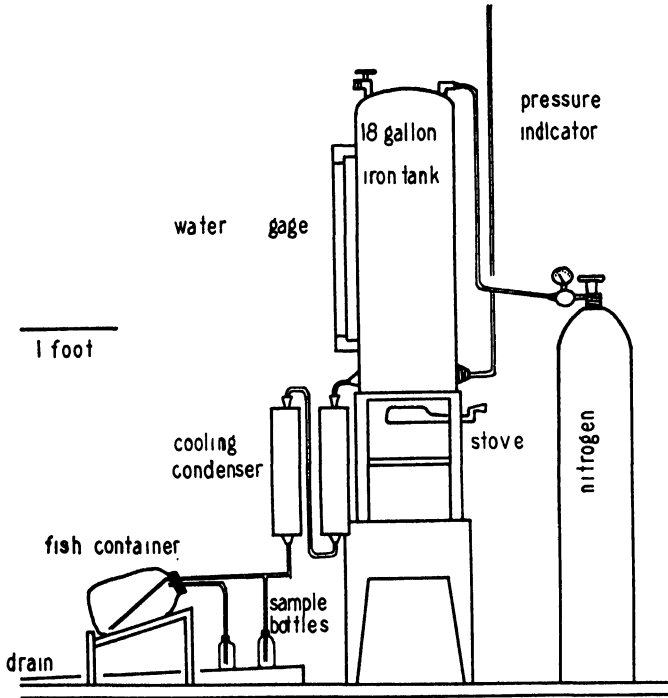


FIG. 4. Diagram of the apparatus used to produce water low in oxygen.

TABLE IV. *Results of 16 battery jar and 23 running water experiments using 231 blunt-nosed minnows. Boiled and aerated water was used in the battery jars*

Asphyxial oxygen in p.p.m.	Battery jar experiments pH 6.8-8.7 temp. 20°-26° C. average final CO ₂ 12.4 p.p.m. average duration 14.5 hrs.		Running water method pH 7.4-8.0 temp. 19°-22° C. final CO ₂ 0.0 average duration 3.2 hrs.	
	No. fish alive	No. fish asphyxiated	No. fish alive	No. fish asphyxiated
0.51-0.75	3	3	0	7
0.76-1.00	0	4	27	53
1.01-1.25	12	10	47	36
1.26-1.50	23	21	108	31
1.51-1.75	12	7	49	9
1.76-2.00	3	4	25	11
2.01-2.25	102	0	129	0

dition of tap water of known oxygen content, it was possible to raise the oxygen concentration in the tank to within 0.2 p.p.m. plus or minus, of the desired point. It was impossible, however, to keep the oxygen value constant for more than four hours because of the diffusion of the dissolved oxygen from the water into the nitrogen. Tap water had to be added to again raise the oxygen to the desired value. It was the original purpose in constructing the apparatus to keep the fish alive for a period of twenty hours in an oxygen

concentration as low as they could tolerate. The original purpose was not fulfilled but significant data are presented below.

Wiebe *et al.* ('34) show that the blunt-nosed minnow is able to extract oxygen to a value slightly less than 1.00 p.p.m. from water having a pH range of 7.0 to 8.0, and temperature range of 18° to 19° C. A series of six experiments using 102 blunt-nosed minnows in 16 battery jars were conducted under conditions similar to those of Wiebe, with the exceptions that water previously heated and aeriated was used, and the final analyses were made when one or more fish showed evidence of asphyxia. The heated water was used in order to determine if water thus treated had any toxic effects. The results are plotted in figure 3 and table IV. The original pH ranged from 7.6 to 8.7, in these experiments, and the final pH ranged from 6.8 to 6.9, the alkalinity having been reduced by the waste products of the fish. The temperature varied between 20° and 26° C. and the duration of the experiments from 8.2 to 54 hours. The average length of the fish was 48.4 mm. and the average weight 0.77 grams. The recorded data show that there was no correlation between the temperature, the duration of the experiment, and the asphyxial oxygen concentration. The curve (Fig. 3) shows that 97 per cent of the fish apparently were in good condition when the oxygen concentration was 2.00 p.p.m., and that the per cent of fish asphyxiated below that concentration rapidly increased. The final carbon dioxide concentration ranged from 8.15 to 23.85 p.p.m. The data show that there is no correlation between the oxygen threshold and the carbon dioxide present. These results raise a question concerning the validity of the statement of Wells ('18) who said, "It is doubtful if any fish could continue to live in water where the carbon dioxide averaged as high as 6 cc. per liter throughout the year." The data from these experiments are probably more critical than those of Wells ('13) because he introduced the fish into water containing lethal concentrations of oxygen and carbon dioxide and noted the survival time of the fish.

Running water low in oxygen was employed in 23 experiments using 129 blunt-nosed minnows. The minnows were placed in 1300 cc. Erlenmeyer flasks containing fresh tap water in the first 11 experiments; and in the 12 remaining experiments, they were placed in a one-gallon jug. The tap water was replaced, at the rate of three liters per hour, by a flow of water low in oxygen. Analyses of carbon dioxide, pH, temperature and oxygen were taken at intervals and when the fish showed evidence of asphyxia. The oxygen concentration in the tank was gradually raised throughout the series of experiments and controlled to a more or less constant value. The results of the 23 experiments show that the minnows were able to live for approximately four hours in a concentration of 1.50 to 1.75 p.p.m. The results of four experiments show that 25 fish were kept alive for 8 to 10 hours in a concentration of 1.75 to 2.00 p.p.m. It was observed, however, that these fish were sluggish and did not respond rapidly to taps on the jug.

The curve (Fig. 3) shows that all of the fish were alive in an oxygen

concentration of 2.00 p.p.m., temperature 19.3° to 22.4° C., pH 7.4 to 8.0, and carbon dioxide 0.0, but as the oxygen content was lowered, there was a sharp decrease in the percentage of fish alive. It is noted that 85 per cent were alive when the oxygen was 1.50 p.p.m., but only 30 per cent were alive at a concentration of 1.00 p.p.m.

When the curve for the above experiments using running water low in oxygen is compared to the curve for the series using heated water in battery jars, it is noted that they show a close agreement, although the conditions of the experiments differ, especially in regards to carbon dioxide content. As previously mentioned, some of the fish used in the series of experiments using tap water in battery jars were tested soon after their capture, and assuming that 10 per cent died from injuries caused by handling, then the curve obtained by this method is similar to the curves mentioned above, and the oxygen threshold for the blunt-nosed minnow in these three experiments is 2.25 p.p.m. The original pH had no effect upon the fish, for the asphyxial oxygen concentration was the same in the experiments where the original pH was 9.0 as it was where the original pH was 7.0. The temperature of these experiments ranged from 20° to 26° C. In the experiments where the temperature ranged from 7° to 12° C. the oxygen threshold for these fish was found to be 1.75 p.p.m., thus indicating that the fish are capable of extracting the oxygen to a lower concentration when the temperature is reduced.

Thompson ('25) made an investigation of the Illinois River in the winter to find the correlation between low oxygen concentration and fish populations. He based his conclusions on the oxygen analyses made in areas where fish were being caught in hoopnets, where fish had recently been caught but had vacated, and where fish were dying or coming to the surface in distress. His general conclusion, "It seems certain that oxygen of 0.0 to 2.5 p.p.m. will kill any of the fish," is in close agreement with the results of these experiments.

SUMMARY

1. Two methods of approach were used to find the asphyxial oxygen point for three species of fish. The fish reduced the oxygen supply by their respiration in one of the methods, and water containing a small amount of oxygen flowed through flasks containing fish in the second method.

2. The time required to reduce the oxygen value of the water to an asphyxial concentration differed considerably in the two methods of experiment. However, the asphyxial oxygen value was found to be approximately the same regardless of the duration of the experiment.

3. The carbon dioxide content and the range of pH had no apparent effect upon the asphyxial oxygen concentration.

4. The fish were capable of reducing the oxygen concentration to a lower level when the temperature was reduced.

5. A large amount of individual variation was encountered in each species

of fish, although they were of a similar size and under the same experimental conditions.

6. The minimum amount of dissolved oxygen tolerated by the yellow perch, steel-colored shiner, and blunt-nosed minnow was found to be 2.25 p.p.m. at a temperature range of 20° to 26° C.

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A POSTGLACIAL FOREST IN CENTRAL NEW YORK¹

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In recent years studies of pollen deposits in bogs have disclosed valuable information relative to the forests of past centuries. Forest trees, being in the main wind pollinated, produce immense quantities of pollen, much of which falls in undrained depressions. As bogs develop and bog formation continues, succeeding layers of pollen are incorporated into successive layers of peat. Such pollen does not decay readily; therefore, analyses of a vertical series of samples of such pollen-containing peat make it possible to trace the history of the succession of different kinds of trees composing the neighboring forests, from the time when the bog was established.

In Europe this type of investigation has been going forward about 20 years and its extensive literature has been listed by Erdtman ('27-'34). In North America, studies listed by Sears ('35) have been carried on chiefly since 1927. So far as is known this report is the first to be concerned with pollen deposits in a peat bog in New York State. The purpose of this paper is to trace the development of postglacial forests in central New York through identification of such bog-preserved pollen.

The bog chosen for this investigation is a small swampy area known as Sandy Ridge Bog, which lies 12 miles north of Syracuse and 3 miles east of the village of Phoenix. The terrain in the neighborhood of Sandy Ridge is a sand flat 400 feet in elevation, broken by drumlins and wave-washed remnants of glacial ridges, extending to Lake Ontario (Fairchild, '07). The land was once inundated by glacial Lake Iroquois (fig. 1). The bog is a remnant of this glacial lake lying in a typical depression about 30 feet below the surrounding land. It is approximately one-half by one-quarter mile in extent, with a rapidly decreasing area of open water 40 feet across, near the center of the bog.

Sandy Ridge Bog lies in vegetation zone B of New York State, as defined by Bray ('30), a zone characterized by *Castanea*, *Quercus*, *Carya*, and *Liriodendron*. On the surface of the bog are some scattered, stunted *Picea mariana*. The dominant species surrounding the bog are: *Acer rubrum*, *A.*

¹ A graduate study under the direction of Dr. Henry F. A. Meier, Head of the Department of Forest Botany and Pathology, New York State College of Forestry, to whom I am indebted for assistance and advice during the course of the investigation. Grateful acknowledgment is also given to Dr. Paul B. Sears of the University of Oklahoma and Dr. George D. Fuller of the University of Chicago for a critical reading of the manuscript.

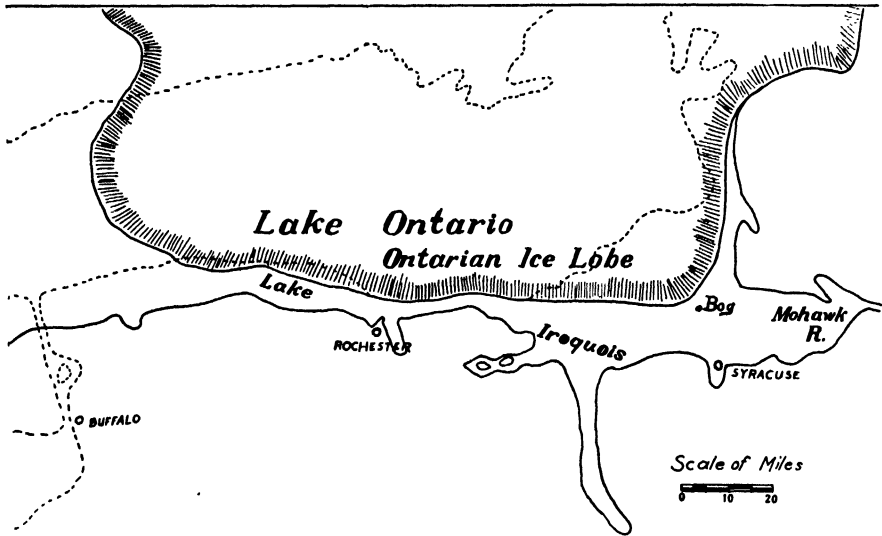


FIG. 1. Lake Iroquois (adapted from Fairchild).

saccharum, *Pinus strobus*, *Populus grandidentata*, *P. tremuloides*, *Quercus bicolor*, *Q. borealis* var. *maxima*, and *Tsuga canadensis*. Subordinate adjacent species are: *Acer pennsylvanicum*, *Amelanchier canadensis*, *Castanea dentata*, *Fagus americana*, *Ilex verticillata*, *Ostrya virginiana*, and *Prunus serotina*. Within a radius of 10 miles the following species, although not abundant, are potential contributors to the bog pollen: *Alnus incana*, *Betula lutea*, *Carya cordiformis*, *C. ovata*, *Thuja occidentalis*, *Fraxinus nigra*, *Juglans cinerea*, *Juniperus virginiana*, *Liriodendron tulipifera*, *Magnolia acuminata*, *Nyssa sylvatica*, *Quercus macrocarpa*, *Q. velutina*, *Salix bebbiana*, *S. discolor*, *Sassafras variifolium*, *Tilia americana*, and *Ulmus americana*.

The study of forest succession through fossil pollen analysis is based on these principles: distribution of wind-blown pollen through a vegetational area is more or less uniform; the type of pollen is definite for each family and sometimes for genera and even for species (Cooke, Lewis and Patrick, '34); the substantial wall of pollen grains of most species resists decay.

In tracing the relationship of fossil pollen to the former forest it is necessary to consider differences in pollen (1) production, (2) transport, (3) reception, and (4) decay.

(1) All trees do not produce the same quantity of pollen. Godwin ('34) cites from Hesmer the following series of diminishing pollen production: *Pinus*, *Corylus*, *Alnus*, *Betula*, *Carpinus*, *Abies*, *Picea*, *Fagus*, *Quercus*, *Tilia*.

(2) The prevailing thought concerning transport indicates that coniferous pollen, equipped with wings, will travel farther than that of non-winged pollen from angiosperm trees. The writer has found pollen abundant in sea water at a distance of 65 miles from a coastal forest of *Picea sitchensis* and *Tsuga*

heterophylla. Stakman ('23) has found pollen floating in the air up to 10,000 feet. Widespread transport assures that the record will be indicative of conditions over a broad territory and not just the reflection of a local situation.

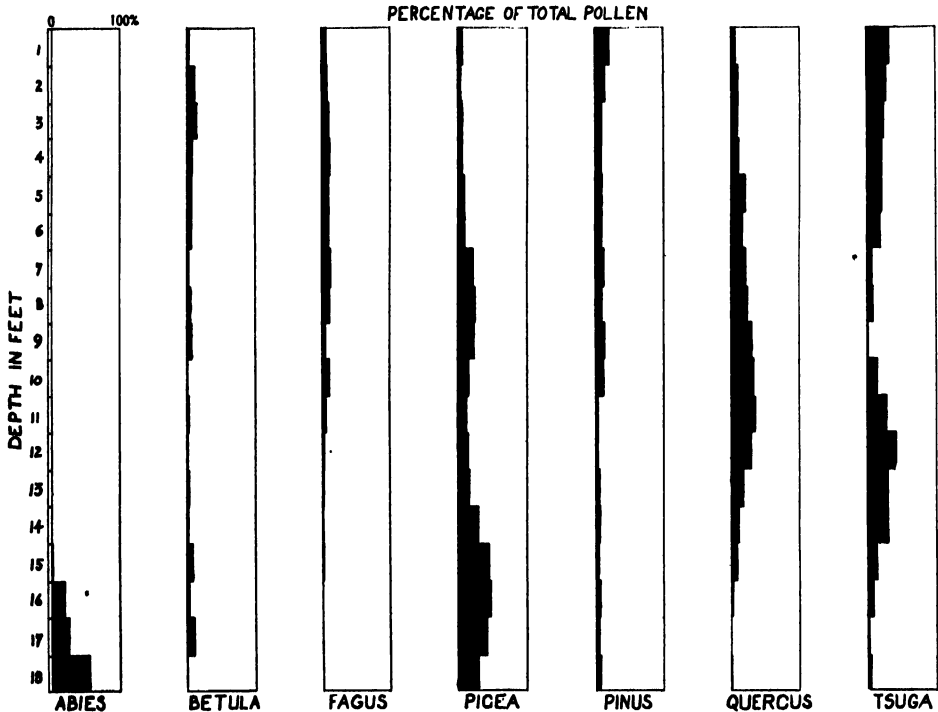


FIG. 2. Graphic representation of the distribution of tree pollen throughout the bog.

(3) Reception. Erdtman, in Wodehouse ('35) says, "If the bog into which the pollen fell were not in proper condition to receive and preserve pollen, it would be lost, and thus no record would remain. Such conditions include a chemical or bacterial state of the water, causing decay; a frozen surface over the bog at the time of pollen shedding. . . ." Another factor might be the draining off of surface water which would carry the pollen away.

(4) Decay. Godwin ('34) points out that *Quercus* pollen decays readily; Lewis and Cocke ('29) note that *Thuja*, *Juniperus*, and *Populus* pollen also break down rapidly; Fuller ('35) says that pollen of *Taxus* and *Larix* are seldom well preserved. In Sandy Ridge Bog it was found that in spite of the abundance of *Populus* in the adjoining woods, no grains were discovered in the peat. Only one grain of *Acer* was found although the genus was well represented in the neighboring forest. Despite the fact that dense stands of *Castanea dentata* were adjacent to the bog before the species was exterminated by chestnut blight, no pollen of this tree was found.

METHODS OF INVESTIGATION

Comparison material. Fresh pollen mounts were prepared according to the methyl-green glycerine method of Wodehouse ('33) for purposes of comparison with the fossil pollen. Further information was obtained from the drawings of grains by Sears ('30a), Wodehouse ('35), Godwin ('34) and Lewis and Cocke ('29). A certain number of pollen grains could not be identified. Presence of these unknown grains was not considered to invalidate the findings of the investigation since they were not sufficiently numerous to be significant.

Sampling. Eighteen peat samples, taken at intervals of one foot with a Davis peat sampler (Bowman, '31), were used for this study. At the 18-foot level, impenetrable glacial sand was encountered. To prevent the mixing of peat from different levels, no two samples were taken from the same bore. As soon as the samples were removed from the tube, they were placed in small vials with a threaded bakelite cap. Each vial was numbered to correspond with the record and then placed in cold storage until needed.

Preparation of material for microscopic examination. Separating pollen from peat was accomplished by mechanical dispersion, using an electric mixing machine of the type employed by Bouyoucos ('27) in dispersing soils. It is a drink-mixing machine with a metal cup such as that commonly used at soda fountains. A cup with four baffle plates, designed by Bouyoucos, was found to be effective in dissociating the peat. Pollen grains because of their minute size and light weight are not destroyed or distorted in this process. The details of mechanical dispersion are as follows: .4 gram of peat was placed in the cup together with 40 cc. of distilled water and three drops of one per cent water-soluble safranin. With the lower, more dissociated strata, 10 minutes agitation was found to be ample time to separate the pollens from the multiple components of the peat mass. From 20 to 30 minutes were required, however, for separation of the strongly fibrous peat in the upper layers. In actual operation, the cup was blocked up so that the bottom of the vessel was within a millimeter clearance of the agitator, ensuring more thorough mixing.

After agitation the 40 cc. of suspension was divided between the two glass centrifuge tubes. Four centrifuge tubes were available, which made it possible to run two separate samples at the same time.

The centrifuge² was operated for one-half hour at a speed of 3600 revolutions per minute. With 20 grams of suspension this rate gave a sedimentation force of approximately 57,000 times gravity at the tip of the tube.³

The supernatant liquid was decanted until only sufficient water remained to make a volume of 10 cc. Examinations of the decanted liquid showed no pollen to be present after one-half hour in the centrifuge. Four-tenths of a gram of peat in 10 cc. of water was found to be a satisfactory dilution. In

² Size 1, Type SB, International Equipment Company.

³ Data from manufacturer.

mounting the centrifuged material the top layer of the sediment was used in each case. Grains were sufficiently numerous on a microscope slide, and at the same time sufficiently free of umbrageous material to permit ready detection of the pollen. Pieces of sphagnum and other vegetable material took the safranin stain and appeared red or pink; the pollen grains remained distinctly yellow or light brown.

Material from the 10-foot level required a different technique. Relatively little vegetable material was present as compared with the other samples, and it was extremely difficult to separate the pollen from the sand. Material could not be mounted satisfactorily under a cover glass until the sand was removed. This was accomplished by mixing the sample with a larger quantity of water and lowering the bottom of the cup one-quarter inch from the agitator to avoid cutting. After thorough mixing, the contents of the cup were quickly emptied on a cheesecloth filter which retained the sand. This was then washed a number of times and the entire filtrate centrifuged. The results were comparable to those obtained at other levels. A pollen frequency of 192 was obtained for the 18-foot level, compared to 188 for the 17-foot level, and 201 for the 16-foot level (table I).

TABLE I. *Percentage of total pollen*

Depth Feet	<i>Abies</i>	<i>Picea</i>	<i>Pinus</i>	Oak	<i>Tsuga</i>	<i>Betula</i>	<i>Fagus</i>	<i>Salix</i>	<i>Ulmus</i>	<i>Tilia</i>	<i>Alnus</i>	<i>Liriodendron</i>	Unknown	Pollen Frequency
1		8.0	21.0	6.0	34.5	3.0	7.5	2.5	6.0	4.5		2.0	5.0	78
2		4.5	15.5	8.5	29.5	10.5	8.0	2.5	6.5	3.5	0.5	1.0	9.5	63
3		5.5	10.0	9.0	24.5	13.0	10.0	9.0	6.5	3.0			9.5	65
4		6.5	9.5	10.5	23.5	6.5	12.0	4.0	2.5	2.0	8.0		15.0	91
5		9.0	10.0	20.0	21.0	5.5	9.5	1.5	2.5	3.0	6.0		12.0	77
6		9.0	9.5	16.0	20.5	6.0	10.0	3.0	7.5	4.5	3.0		11.0	87
7		22.0	12.0	20.5	7.0	2.5	13.5	5.0	2.0	3.0	2.5		10.0	99
8		24.5	10.0	22.5	9.0	3.0	11.5	7.5	3.5	2.5	1.0		4.5	104
9		22.5	13.0	29.0	2.0	3.5	4.5	5.0	8.5	2.0	1.5		8.5	108
10		14.5	10.5	32.0	15.5	1.5	9.5		4.5	4.5	1.5		6.0	105
11		12.0	2.5	34.5	27.5	2.5	5.0	4.5	4.5	2.5	1.5		3.0	98
12		15.0	2.5	28.0	31.5	0.5	2.5	10.5	1.5	4.0	1.5		2.5	111
13		16.5	5.5	21.5	30.0	2.5	1.5	9.5	1.5	4.0	0.5		7.0	126
14		28.5	6.5	13.0	30.0	1.5	0.5	9.0	2.0	1.0	1.0		7.0	120
15	.5	45.0	5.0	7.5	14.0	7.0	2.5	6.5		0.5	4.5		7.0	141
16	19.0	47.0	5.5	2.5	8.0	2.5		6.0	1.5	1.5			6.5	201
17	25.0	43.0	5.0		2.0	10.5		9.0					5.5	188
18	56.5	29.5	6.0	0.5	3.5								4.0	192

Counting. In view of the small number of significant species, a count of 200 grains was fixed upon as adequate to give a representative picture of the forest composition (table I). This assumption is fortified by Barkley ('34). Six mounts was the minimum established for each level. The number of pollen grains per square centimeter of slide surface was calculated at each level to give the pollen frequency values shown in table I.

Concentration of the grains in the upper portion of the bog is much less

than in the lower, due, perhaps, to packing of the peat materials as they settle. To avoid an error by taking a count from the part of a sample in which grains of one species accidentally might be concentrated, two precautions were observed: (1) the entire sample from each level was thoroughly mixed, and a representative piece weighed out from it; (2) in the lowest six feet, double the number of grains was counted, then averaged. No great disparity was discovered between any two counts made at the same level.

CONCLUSIONS

The 18-foot level possesses such an overwhelming quantity of *Abies* and *Picea* pollens that it is logical to assume the presence of *Abies-Picea* forests here at the time the bog was forming. Pollen from these stands would undoubtedly accumulate in large quantities in pools in the Lake Iroquois-Lake Ontario Basin following recession of the ice. The present northern habitat of *Abies* was at that time covered by ice, and if other distant forests of *Abies* were responsible for the deposition of that pollen, it should be found throughout the upper layers of peat. Such is not the case and the conclusion is ineluctable that an extensive *Abies-Picea* forest occupied this area in the early stages of bog formation. It will be noticed from table I that, moving from the bottom of the bog toward the surface, *Abies* pollen disappears rapidly, whereas *Picea* pollen is present continuously from bottom to top (fig. 2). This is assumed to be an expression of over-representation of the genus due to incidence of *Picea mariana* growing directly on the bog, and the consequent deposition of its pollen in much larger percentage than is warranted by its numerical proportion in the forest as a whole. *Picea* is not abundant in the region now, and occurs only in bogs as small stunted trees. The pollen from these would not be as subject to wide dissemination by the wind, as that of other trees situated upon the ridges.

At the 17-foot level, retreat of *Abies* is apparently well under way but the forest is still dominantly coniferous (approximately 70%). Species within the genus *Betula* and the genus *Salix* respectively, are not separable by their pollen. It is possible that the relatively large representation of both genera at the 17-foot level may be due to boreal forms such as *Betula glandulosa* and *Salix speciosa*, no longer native to the Sandy Ridge area.

Definite encroachment of the hardwoods is shown in the 16-foot level by the occurrence of *Quercus*, *Ulmus*, and *Tilia* pollen with a further decline in *Abies* pollen. It will be noticed from table I or figure 2 that *Pinus* is more or less static at the lower levels, decreases to a minimum of 2.5 per cent at 12 and 11 feet, then increases to a maximum of 21 per cent at the one-foot level. The writer is of the opinion that the *Pinus* pollen of the 11-foot level and lower is probably *P. banksiana*, and that from 10 feet to the surface, *P. strobus*. At the 15-foot level *Abies* pollen was found to be poorly represented, while that of the hardwoods had increased in number and variety with the

addition of *Ulmus* and *Fagus*. From this point up to the surface the record is one of increasing dominance of the hardwoods with variations in numbers of different species at different levels. *Quercus*, *Tsuga*, and *Liriodendron* as well as *Abies* and *Picea*, show sufficiently definite fluctuations (table I) to merit mention. *Quercus* advances to a maximum at 11 feet, then regresses slowly. *Tsuga* reaches a peak at 11 feet, falls away to a minimum at 9 feet, then again rises to a dominance as the surface is approached. This final decrease in abundance of *Quercus* and increase of *Tsuga* is in keeping with the succession of forests in central New York. The same *Quercus* climax has been found by other investigators in practically all bogs examined along the present northern boundary of the deciduous forest from Minnesota east to Quebec. *Fagus*, *Acer*, and *Tsuga* are the most mesophytic types, gradually replacing other genera such as *Quercus* and *Pinus*. With reference to this particular record, however, it should be noted that *Tsuga* is apparently over-represented in the pollen horizon. Its pollen percentage in the upper foot greatly outnumbers the percentage of *Tsuga* trees in the adjacent forests. Finally, *Liriodendron*, absent in the lower layers, but appearing in small quantities in the upper layers, is assumed to be an indication of its recent establishment in this part of the country. Two small stands within a few miles of Sandy Ridge Bog are the most northerly representatives of the species in this area, which is slightly north of the normal range of *Liriodendron*.

SUMMARY

Peat from a bog near Syracuse, N. Y., was examined to determine its content of forest tree pollen.

Separation of the pollen from the peat was accomplished by mechanical dispersion rather than by the chemical means usually employed.

Pollens of *Abies* and *Picea* were found in great abundance in the lowest layers, the former diminishing very rapidly from the 18-foot to the 15-foot level, above which none was found. *Picea* pollen decreased more slowly, but persisted throughout all the levels. Various hardwood pollens, scarce or absent in the lower layers, were numerous and more varied in the upper layers.

The pollen deposits give evidence of a postglacial coniferous forest which was gradually replaced by hardwoods. This change was concomitant with the development of forests in other states south of the Great Lakes (Patzger, '32; Sears, '30; Voss, '34).

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ANALYSIS OF THE POPULATIONS OF FISH IN THE WATERS OF THE MASON GAME FARM, MASON, MICHIGAN¹

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The waters of the Mason Game Farm consist of an artificial pond eight and one-half acres in area and two small streams which converge before flowing into the pond. The farm and pond are utilized by the Department of Conservation to rear game birds.

In the fall of 1937 the pond was drained to facilitate repair of some of the pens, and if possible, to eradicate the goldfish which had become abundant. Fishing was poor and the large numbers of goldfish, and other fish unsuited for angling, were considered a possible cause of the scarcity of desirable fishes. After the pond had been drained, the fish in a section of each of the two streams were killed by poisoning and were collected.

This discussion represents a study of the fish which were present in the two creeks and in the pond. According to the Game Farm personnel, few or no bait minnows had been seined from the streams and few fish had been removed from the pond in recent years. Each of the waters was presumably supporting a maximum fish population at the time of the poisoning. Since the fish had ready access to each of the three different waters, it might be assumed that each species chose the type of habitat best suited to it. There is a possibility, of course, that some of them may not have selected their most desirable habitats because of competition.

In addition to a comparison of the populations in the three waters, data were obtained on the total number, kind and weight of fish in the two streams at the time of the original poisoning and again forty days after that date. The second study was made to determine what number and species had re-entered the sections from which all fish had been removed.

The fish were preserved in formalin and studied after preservation. They were weighed on a Welch balance by species but not by individuals. References to the literature on the ecology and life history of the several species have been limited to a very few publications, for even a brief reference to the literature on the subject would involve some pages of discussion. Each of the streams and the pond with their populations are considered separately.

BIG MUD CREEK

The portion of Big Mud Creek studied includes an 850 foot section of the stream just above the confluence of this creek and Little Mud Creek.

¹ Contribution from the Institute for Fisheries Research, Michigan Department of Conservation and University of Michigan.

The section has an area of 0.15 acres at periods of relatively low water and an average width of about 7.5 feet. It is a slow moving stream with numerous pools. The bottom is chiefly of sand and gravel. At the time the fish were removed, the water was low. The flow was approximately 60 gallons per minute, determined by placing a temporary dam in the stream and passing all water over it in pails for a period of approximately 10 minutes. The upper portion (about half) of the stream section flows through an open pasture and in this area considerable aquatic vegetation is present. The lower half flows through timber and is devoid of vegetation. When the stream was examined (September 30 and October 1, 1937), the water was relatively clear and the name given this stream seemed to be decidedly misleading.

Between 1921 and 1926 4,000 brook trout, 48,000 rainbow trout and 35,000 brown trout, chiefly as fry, were introduced into Big and Little Mud Creeks. This stocking was unsuccessful. Summer temperature records are not available, but the streams probably become too warm to support trout.

On the morning of September 30th a seine was placed across the stream at the outlet of Little Mud Creek and another at the upper end of the 850 foot section (see map). About 0.8 pound of powdered derris root (5 per cent rotenone content) was mixed with water and placed in the stream just below the upper net. The stream was impounded at this place for a few minutes prior to the introduction of the poison. After the fish showed active distress in the temporary pool, the water was released. All fish in the section were probably killed, since no live specimens were found later and since the bullheads, which are very resistant to derris root, were found to be dead.

Efforts were made to recover every fish on the day and the succeeding day of the poisoning. Some fish undoubtedly were not recovered even though numerous collecting trips were made up and down stream, but a very large percentage of them were obtained. It is believed that those picked up represent fully 90 per cent of the total population.

A total of 3,872 fish, representing 13 species, was collected. Darters, because of their small size and failure to float after being killed, were probably less thoroughly collected than were the other species. The population collected had a total weight of 11,305 grams or 24.9 pounds. The number of fish of each species, the percentage of the entire population represented by each species, and the total weight by species are listed in table I.

Almost a third of the fish were creek chubs (*Semotilus atromaculatus atromaculatus*); Johnny darters (*Boleosoma nigrum nigrum*) were second in abundance, and blunt-nosed minnows (*Hyborhynchus notatus*) were third. Mud minnows (*Umbra limi*), black-nosed dace (*Rhinichthys atratulus melea-gris*) and stone-roller minnows (*Camptostoma anomalum pullum*) were each represented by 300 to 400 specimens. The other seven species were present in relatively small numbers.

On November 9th, 40 days after the original study, the same area was poisoned in a similar way except that larger quantities of derris root were

used, since the stream had a somewhat greater flow at this time. Again all fish were probably killed and almost all were recovered. Two hundred and four specimens having a total weight of 972 grams were collected. The data, by species, are recorded in table I.

TABLE I. *Species, weight and number of fish taken from a 850 foot section of Big Mud Creek on September 30th and October 1st, 1937, and from the same section on November 9, 1937*

Species	Taken Sept. 30 and Oct. 1			Taken Nov. 9		
	Number	Per Cent	Total Weight (Grams)	Number	Per Cent	Total Weight (Grams)
White sucker	19	0.5	143	3	1.5	56
Goldfish	1	—	1	1	0.5	2
Black-nosed dace	346	8.9	858	8	3.9	28
Creek chub	1,158	29.9	6,490	74	36.3	506
Golden shiner	2	0.1	3	—	—	—
Common shiner	26	0.7	213	14	6.9	15
Blunt-nosed minnow	618	16.0	638	34	16.7	66
Stone-roller minnow	321	8.3	1,294	—	—	—
Yellow bullhead	42	1.1	194	3	1.5	11
Mud minnow	399	10.3	572	51	25.0	69
Mud pickerel	15	0.4	342	7	3.4	205
Johnny darter	922	23.8	548	6	2.9	9
Pumpkinseed	3	0.1	9	3	1.5	5
Totals	3,872	100.0	11,305	204	100.0	972

Some species obviously migrated into the area much more than did others. Of the six most common species, creek chubs and mud minnows represented a greater proportion of the total percentage than they had at the time of the original poisoning; the percentage of blunt-nosed minnows was approximately the same as previously, and the percentage of black-nosed dace, stone-roller minnows and Johnny darters decidedly declined. Stone-rollers showed no movement into the area and Johnny darters, which were well represented originally, were almost entirely absent at the second poisoning. A study of table I suggests that certain species (creek chubs and mud minnows) have wide movements at this time of year and that others (stone-rollers and Johnny darters) are relatively sedentary.

Three species taken at the time of the second poisoning had a larger average size than those killed on September 30th. Black-nosed dace had increased in average weight from 2.5 grams to 3.5 grams, creek chubs from 5.6 grams to 6.8 grams, and blunt-nosed minnows from 1.0 gram to 1.9 grams. Mud minnows had a similar average weight each time. Whether the larger specimens tended to migrate more than the smaller ones, or whether the difference in weight may be attributed to growth during the forty day period, was not determined.

LITTLE MUD CREEK

The section of Little Mud Creek which was used for the fish population study differs decidedly from the portion of Big Mud Creek mentioned above. The water is more rapid, and the pools are fewer. Vegetation is absent and the bottom is sand, covered in a few areas by a thin layer of organic soil. On September 30th the water temperature was 54° F. at 9:30 A.M. (air 68°), compared with 69° for Big Mud Creek at 3:00 P.M. (air 81°). Temperatures were not taken at identical times, but Little Mud Creek was undoubtedly the cooler. By the same method used for Big Mud Creek, the flow at the time of the study was calculated as being about 50 gallons per minute. The average width was approximately 4 feet. The portion of the stream which was studied consisted of the lower 1,150 feet having an area of 0.09 acres, all of which flows through a wooded region and is generally shaded.

Methods of obtaining the population were identical with those used for Big Mud Creek. The two studies were made at the same time and equal amounts of derris root were used.

In the original population study 987 fish weighing a total of 2,691 grams (5.9 pounds) were taken. The fish (see table II) were primarily creek

TABLE II. *Species, weight and number of fish taken from a 1,150 foot section of Little Mud Creek on September 30th and October 1st, 1937, and from the same section on November 9th, 1937*

Species	Taken Sept. 30 and Oct. 1			Taken Nov. 9		
	Number	Per Cent	Total Weight (Grams)	Number	Per Cent	Total Weight (Grams)
Brook lamprey	26	2.6	108	—	—	—
White sucker	—	—	—	1	1.1	27
Black-nosed dace	102	10.3	311	4	4.2	19
Creek chub	419	42.5	1,613	76	80.0	558
Common shiner	—	—	—	3	3.2	10
Blunt-nosed minnow	—	—	—	1	1.1	3
Stone-roller minnow	3	0.3	9	—	—	—
Mud minnow	333	33.7	432	8	8.4	25
Mud pickerel	10	1.0	120	1	1.1	15
Johnny darter	94	9.5	98	—	—	—
Common sunfish	—	—	—	1	1.1	4
Totals	987	100.0	2,691	95	100.0	661

chubs and mud minnows. Black-nosed dace and Johnny darters each represented about ten per cent of the population. Brook lampreys (*Lampetra lamottenii*), mud pickerel (*Esox vermiculatus*) and stone-roller minnows comprised the remainder of the population.

When the fish were poisoned 40 days later, 95 specimens weighing 661 grams were recovered. Eighty per cent of these fish were creek chubs. Mud minnows comprised 8.4 per cent of the population. Six other species were

taken. As in Big Mud Creek, the creek chubs comprised a greater percentage of the total population on the second study than they did on the first examination. Mud minnows, however, were relatively fewer at the time of the second poisoning. As in the other stream, Johnny darters and stone-roller minnows showed little or no movement into the area during the 40 day period.

Four species, white suckers (*Catostomus commersonnii commersonnii*), common shiners (*Notropis cornutus frontalis*), blunt-nosed minnows and pumpkinseeds (*Eupomotis gibbosus*), were present in very limited numbers in the second study but were not taken in the original examination.

Twenty-six brook lampreys were recovered after the poisoning on September 30th. All except one of these were taken on the second day (October 1) and some were still alive, though incapacitated, when collected. Many of these lampreys may have remained in the bottom and the actual percentage of the lamprey population represented by those collected is not known. Since none were taken in the second poisoning, which was more concentrated than the first, all may have been killed in the September 30th poisoning.

Originally the creek chubs had an average weight of 3.8 grams; those taken 40 days later averaged 7.3 grams. Mud minnows originally weighed 1.3 grams each, but the eight specimens taken 40 days later average 3.1 grams each. It seems that the larger fish tend to migrate more than the smaller ones, since these very large differences can hardly be attributed entirely to growth.

COMPARISON OF THE TWO STREAM POPULATIONS

The two populations were taken from streams which differed ecologically as indicated above. In table III the two populations are compared on a per

TABLE III. Number of fish per acre in Big Mud Creek and Little Mud Creek in the sections from which the fish were removed, September 30th and October 1st, 1937

Species	Number	
	Big Mud Creek	Little Mud Creek
Brook lamprey	—	289
White sucker	127	—
Goldfish	7	—
Black-nosed dace	2,318	1,132
Creek chub	7,759	4,651
Common shiner	174	—
Golden shiner	13	—
Blunt-nosed minnow	4,141	—
Stone-roller minnow	2,151	33
Yellow bullhead	281	—
Mud minnow	2,673	3,696
Mud pickerel	101	111
Johnny darter	6,177	1,043
Pumpkinseed	20	—
Total	25,942	10,955

acre basis. The larger, slower, warmer stream, with vegetation in a portion of it, contained 13 species, compared with 7 species in Little Mud Creek; it

also contained about $2\frac{1}{2}$ times the number of fish per unit of area found in the smaller stream. In pounds of fish per acre, the larger stream was decidedly the more productive, for the two streams contained 166.2 pounds per acre and 65.9 pounds per acre respectively.



FIG. 1. Riffles in Big Mud Creek in pasture.

An examination of table III shows a decided difference in the fish fauna of the two streams. Seven species: white suckers, goldfish (*Carassius auratus*), common shiners, yellow bullheads (*Ameiurus natalis natalis*) and pumpkinseeds, were present only in the larger, slower stream. One species,

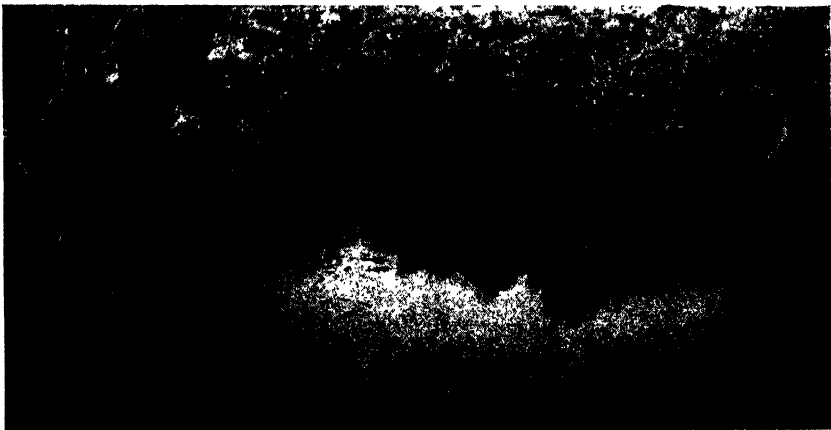


FIG. 2. Pool in Big Mud Creek in pasture.

the brook lamprey, was found in the smaller stream only. Of the fish common to both streams, mud minnows were more abundant (per unit of area) in Little Mud Creek, and mud pickerel were about equally distributed in both.

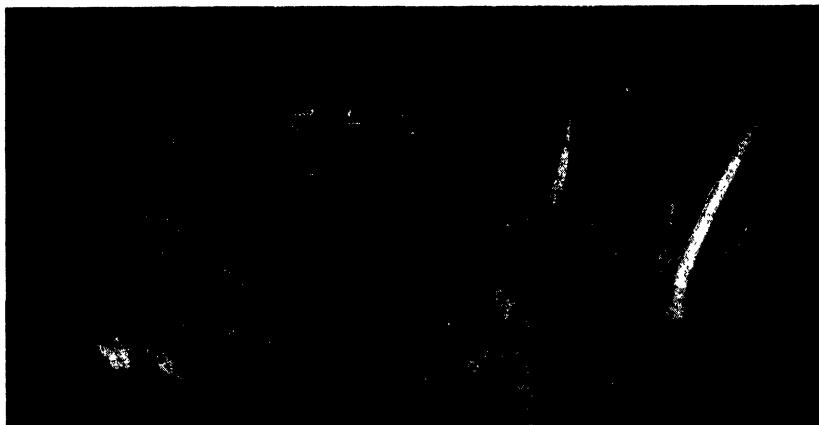


FIG. 3. Big Mud Creek in wooded section.

The other species were more abundant in Big Mud Creek. The blunt-nosed minnow apparently showed extreme preference for Big Mud Creek, since it was abundant there but entirely absent in Little Mud Creek. Stone-rollers were common in the larger stream, but rare in the smaller one. The lower limits of the two streams were only a few feet apart, near the point where Little Mud Creek empties into Big Mud Creek, and the fish had ready access to either stream.

Comparisons were made of the average size of fish of five species common to the two creeks, and these fish were also placed in one-inch size groups. For four of these species (see table IV) the fish in the larger stream had a

TABLE IV. *Comparison of the sizes of fish of each species common to both streams, one inch groups*

Species	Stream	Ave. Wt. (Grams)	Number in Each One Inch Size Group							
			1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9
Black-nosed dace	B.M.C.	2.5	73	270	3	—	—	—	—	—
	L.M.C.	3.0	2	96	4	—	—	—	—	—
Creek chub	B.M.C.	5.6	634	127	191	133	50	11	11	1
	L.M.C.	3.8	209	46	131	32	—	1	—	—
Stone-roller minnow	B.M.C.	4.0	51	138	116	15	1	—	—	—
	L.M.C.	3.0	1	1	1	—	—	—	—	—
Mud minnow	B.M.C.	1.4	309	63	26	1	—	—	—	—
	L.M.C.	1.3	278	35	18	2	—	—	—	—
Mud pickerel	B.M.C.	22.8	—	—	—	—	9	5	1	—
	L.M.C.	12.0	—	—	—	5	5	—	—	—



FIG. 4. Little Mud Creek.

larger average size; black-nosed dace, however, were the larger, on the average, in the smaller stream. Mud minnows had about the same average size in each stream. Creek chubs and mud pickerel were decidedly larger in Bid Mud Creek than in Little Mud Creek. It is improbable that for any of these species the young primarily inhabited one stream and the adults another; such condition is not evident at least from an examination of the size groups (table IV). No attempt was made to determine the rate of growth of the fish in these streams.

MASON GAME FARM POND

The Mason Game Farm Pond was formed by impounding Big Mud Creek. Its upper end is about six hundred feet below the sections of streams discussed in the preceding pages. The pond was originally created to supply water power for operating a small saw mill. Extensive silting has occurred



FIG. 5. Game Farm Pond, after draining.

during the many years that the pond has been in existence and the water is now very shallow. Fully a third of the pond has a depth of about a foot or less, and the greatest depth, at the dam is only about 6 or 7 feet. The average depth is probably not over 3 feet. Vegetation is sparse and consists primarily of yellow pond lilies. Numerous stumps are present in the upper end of this $8\frac{1}{2}$ acre pond.



FIG. 6. View of pond bottom from dam.

Dr. D. L. Caswell, superintendent of the Game Farm, provides the following information regarding the pond, the angling and the stocking of fish.

"According to Roy Hunt [veteran Game Farm employee], the pond at the Game Farm is about 75 years old. Before 1918 the pond was considered a good fishing place, offering catches of bluegills, sunfish, bullheads and pike (northern). In the spring of 1918 the dam was washed out leaving the pond dry except for the stream running across the bottom. In the fall of 1918 the dam was rebuilt. About 1920-1922, two plantings of fingerling smallmouth bass were made (quantity unknown). A few years later Hunt recalls having seen some large bass, whereas, before the planting was made he does not recall having seen any bass.

"About 1926, according to Hunt, 34 goldfish were planted; 30 gold ones and 4 black ones, which are supposed to have been secured from the St. Clair River by nets." . . . "It is my understanding that since 1929 the boards in the dam once gave way and allowed the pond to drain. At that time, it is said, the stream below was literally golden with gold fish."

According to Harry Ruhl, Chief of the Game Division of the Michigan Department of Conservation, fishing was good until 1918 and bluegills (*Helioperca macrochira*) were dominant in the catch but after the pond was restored in 1918 fishing was poor and bullheads were dominant in the catch. The bluegills probably went downstream when the dam broke in 1918 and failed to become re-established later. The bass referred to above may have

gone downstream at the later break. No bluegills or bass were seen when the pond was drained in 1937. An examination of the fish (in 1937) suggested that angling would probably have been uneventful so far as taking fish of catchable size was concerned for very few fish of desirable species or desirable size were present.

Only two species were taken in the pond which were not also present in the stream above. These were black crappies (*Pomoxis sparoides*), which

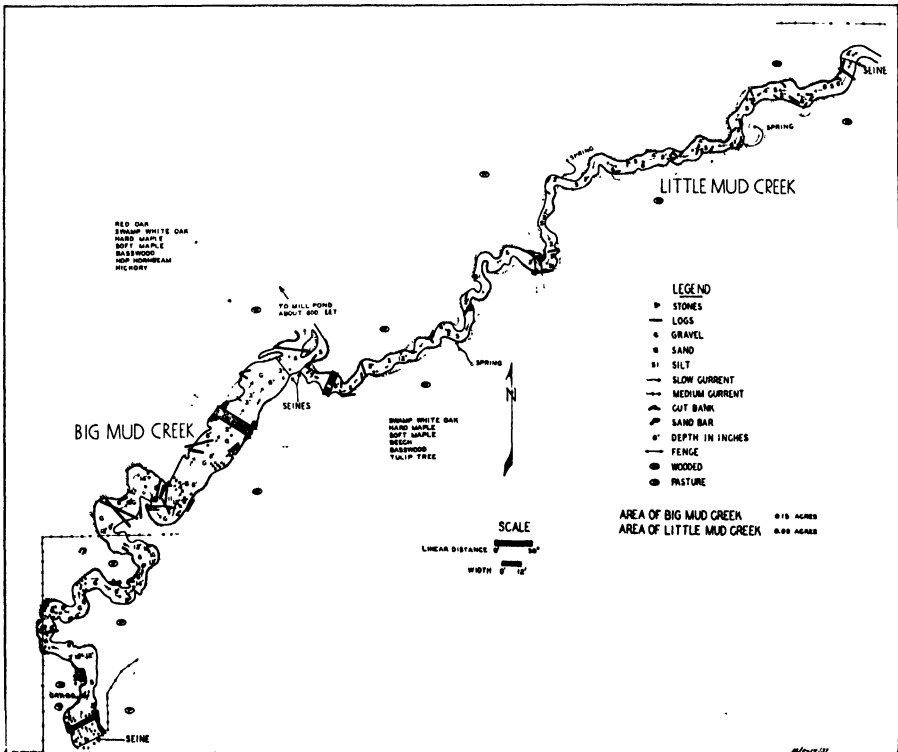


FIG. 7. Map of the sections of Big Mud Creek and Little Mud Creek from which the fish were removed.

were not abundant in the pond, and long-eared sunfish (*Xenotis megalotis peltastes*), which were too small to be of catchable size. Small non-trout streams contain few species which are desirable for angling, or contain only the young or stunted individuals of these species, and when such streams are impounded, stocking to introduce desirable fish is obviously necessary unless these have access from connecting waters.

No accurate account can be given of the number of fish which were present in the pond when it was drained in 1937. Many remained in or on the muddy bottom and many passed down stream. A large number of goldfish were removed by some of the several thousand spectators who came in re-

sponse to a news release indicating that the pond was to be drained and that goldfish would no longer be obtainable from this source after the draining. About 200 gallons of fish were definitely accounted for and these represented only a portion of the total population.

General observation suggests that the pond was decidedly over-populated, for an examination of the fish and of the scales of some of them indicated that the suckers, goldfish and sunfish were stunted. Black crappies were of a relatively large size, but only about a hundred were seen. Small (young) crappies were not in evidence, suggesting that this species may possibly have become extinct in the pond within a few years. Some bullheads were of catchable size, but their abundance cannot be estimated because of the possibility that many may have remained in the muddy bottom. Sunfish were generally too small to be of value, and the other species were worthless for angling.

After most of the water had been drained from the pond, a bag seine was placed in the spillway to catch the fish which had become concentrated at the dam. Twenty gallons of fish obtained by this method included twelve species. This sample was not representative, because many goldfish and some bullheads and crappie had been removed. With the exception of these three species, the relative abundance of fish of each kind in the sample may possibly have been representative of the abundance of these species in the pond.

The species taken in the 20 gallon sample, and the number and percentage of each are given in table V.

TABLE V. *Number and percentage of fish from Mason Game Farm Pond in a 20 gallon sample, September 30th, 1937*

Species	Number	Per Cent of Total Sample
White sucker	787	10
Goldfish	56	1
Creek chub	310	4
Common shiner	260	3
Golden shiner	619	8
Blunt-nosed minnow	4,276	57
Yellow bullhead	52	1
Mud minnow	28	—
Mud pickerel	8	—
Black crappie	1	—
Long-eared sunfish	20	—
Pumpkinseed	169	2
Sunfish (young of the year) ¹	918	12
Total	7,504	98

¹ Both long-eared and pumpkinseed, and perhaps also hybrids of the two, were not sorted by species.

COMPARISON OF THE POND AND THE STREAM POPULATIONS

A comparison cannot be made of the pounds per acre in the streams and in the pond because complete data on the latter are not available. Some

species which had ready access to the pond and the two streams showed decided preference for one or the other of these waters. How much of this was due to population pressure cannot be determined. An examination of tables I, II and V suggests that white suckers showed a decided preference for the pond as did also the goldfish. Creek chubs, on the contrary, were much more common in the streams where they were the most abundant of any species, than in the sample from the pond where they represented only four per cent of the fish. Common shiners and golden shiners (*Notemigonus crysoleucas auratus*) showed a preference for the pond. Black-nosed dace were found only in the streams. Blunt-nosed minnows comprised over half of the fish in the sample from the pond. They were also prominent in Big Mud Creek, but were absent in Little Mud Creek. Stone-roller minnows and Johnny darters were more abundant in the slow running water of Big Mud Creek.

The bullheads taken in the creek were all small; adults were found only in the pond. Mud pickerel were not especially abundant in any of the three waters but were most common, in proportion, in Little Mud Creek. Crappies and sunfish were primarily confined to the impounded water and lampreys were taken only in the smaller stream.

In general the habitats in which the fish were found were in accord with the habitats of the several species as indicated by several authors and as recorded in table VI. The common shiner was relatively more abundant in

TABLE VI. *Habitats of the species found in the Mason Game Farm waters as indicated by the authorities listed*

Species	Habitat	Authority
Brook lamprey	Streams exclusively	Gage
White sucker	Varied	Adams and Hankinson
Goldfish	Lakes and rivers, sluggish water	Hubbs and Cooper
Black-nosed dace	Rapid waters in small creeks	Traver
Creek chub	Small creeks, moderate to rapid water	Hubbs and Cooper
Golden shiner	Lakes, ponds and streams	Hubbs and Cooper
Common shiner	Creeks, clear water	Hubbs and Cooper
Blunt-nosed minnow	Lakes and sluggish streams, sandy shoal	Hubbs and Cooper
Stone-roller	Creeks, gravelly areas	Hubbs and Cooper
Yellow bullhead	Creeks, lowland lakes	Forbes and Richardson
Mud minnow	Sluggish creeks, in abundant vegetation	Adams and Hankinson
Mud pickerel	Creeks, also ponds and small rivers	Forbes and Richardson
Johnny darter	Typically creeks and small brooks	Forbes and Richardson
Pumpkinseed	Ponds, small rivers	Forbes and Richardson
Long-eared sunfish	Chiefly streams	Forbes and Richardson
Black crappie	Varied, lakes in preference to streams	Forbes and Richardson

the pond, although Hubbs and Cooper ('36) indicate its preferred habitat to be creeks with clear water. The yellow bullhead, reported by Forbes and Richardson ('20) to prefer streams in Illinois, showed decided preference for the impounded water. Mud minnows, reported by Adams and Hankinson

('28) to prefer sluggish creeks in abundant vegetation also were present in Little Mud Creek, a moderately fast stream with no vegetation. Descriptions of the habitats are mostly of a general nature and close comparisons cannot be made except possibly for the black-nosed dace. Traver ('29) indicates that this fish inhabits rapid waters in small creeks. The fish was common in Little Mud Creek. In the larger stream it apparently was much more abundant in the upper, narrow, faster portion than in the lower area where the creek is wider and slower.

BAIT MINNOWS

The problem of obtaining bait minnows is becoming more and more acute as the angling pressure increases and as the removal of forage fish for bait from fishing waters becomes more and more discouraged because of the value of these species as food for the game fish. This study was made to determine how many fish were being supported by the two streams and to note changes in the population where the water is impounded. The larger stream carried about 4,000 fish in the section studied, and the smaller stream less than a thousand; per linear foot of stream these represent 4.6 and 0.9 fish respectively.

The fish which might be regarded as bait minnows (white suckers, black-nosed dace, creek chubs, common shiners, golden shiners, blunt-nosed minnows, stone-roller minnows and mud minnows) totaled 2,889 and 857 respectively for Big Mud Creek and Little Mud Creek in the sections studied. Some of the specimens were too small for use as bait minnows. Others, especially creek chubs, were considerably larger than the ordinary bait minnow size. If it be assumed that these fish had a value of one cent each as bait, the standing crop for the sections of the two streams was worth \$28.89 and \$8.57 respectively. The value per acre was about \$192 and \$95 respectively or considerably higher in value than most farm crops. If some of these were removed periodically, the value per year might be much greater for more fish would probably have survived and perhaps growth would have been more rapid. It might be added that, in view of the finding that creek chubs tended to move into an area soon after the fish were removed, it may be possible by rather heavy removal of these fish, to harvest a considerable portion of the fish which grew on the neighbor's property unless he also harvested bait minnows from his area.

The number of forage fish in the pond could not be determined, but was undoubtedly many times the number originally present in the stream. The study suggests that some impoundment of the water would be especially desirable if small, warm streams of this type were to be used to raise forage fish. Observations suggest, too, that shaded portions of the stream are decidedly less productive of forage fish than are those portions which are run through open pasture.

SUMMARY

1. Studies were made of the fish populations in two small streams and a pond, located on the Mason Game Farm, in Mason County, Michigan.
2. In an 850 foot section of the larger stream (Big Mud Creek) 3,872 fish representing 13 species were taken after poisoning with powdered derris root. These fish had a total weight of 24.9 pounds, representing a weight of 166.2 pounds per acre. The section studied has numerous pools and flows at a moderate rate partly though open pasture and partly through woods.
3. When the poisoning was repeated 40 days later, 204 fish were taken from the same area. Certain species, especially creek chubs and mud minnows had repopulated the area to a much greater extent than had other species, notably stone-roller minnows and Johnny darters.
4. In an 1,150 foot section of the smaller stream, Little Mud Creek, a relatively rapid, sandy-bottomed, vegetationless stream flowing entirely through woods, 987 fish weighing 5.9 pounds (65.9 pounds per acre) were taken by the same method used for Big Mud Creek.
5. When the poisoning in Little Mud Creek was repeated 40 days later, 95 fish were taken. Eighty per cent were creek chubs, compared with 42.5 per cent creek chubs in the original study.
6. A comparison was made of the two stream populations, with reference to species, abundance, and size. Some species were relatively more abundant in the larger stream, others in the smaller creek.
7. The Game Farm Pond, formed by impounding the water of the two streams some few hundred feet below their confluence, was drained. Analysis of a 20 gallon sample of fish showed 12 species of fish to be present.
8. A comparison was made of the pond population and the stream populations with reference to species and relative abundance. Only two species, black crappies and long-eared sunfish, were found exclusively in the pond.
9. Few fish of value to angling were present in the pond.
10. At the value of one cent per forage fish of suitable species for bait, the standing crop in Big Mud Creek was worth \$192 per acre; in Little Mud Creek it was worth \$95 per acre.

ACKNOWLEDGMENT

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THE RELATION OF FIRE TO STAND COMPOSITION OF LONGLeAF PINE FORESTS¹

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Forest fires are more common in the region of the longleaf pine, *Pinus palustris* Mill., than in any other portion of the United States. Their frequent occurrence is definitely known to date back for several centuries, as attested by William Bartram ('28) and other early explorers, who reported that fires were often set by hunting parties of Indians in an attempt to corral game. During more recent times, fires have probably been even more numerous than previously. For many years naval-stores operators have intentionally set fire to the woods after hoeing away all inflammable material from the bases of trees being worked for resin. Since each pine tree is protected from the flames by an individually hoed firebreak, the trees usually escape serious stem injury during these fires, and the forest is largely protected against subsequent accidental fires which might destroy valuable naval-stores equipment. In addition to naval-stores operators, cattle owners also have been responsible for a large number of fires, which are set in winter to stimulate the production of early spring forage in the pine woods. Lastly, many of the native populace intentionally burn the woods to remove the heavy accumulation of "rough"² a habit passed down within the family for generations. Until recent years, because of the frequent occurrence of fires in the region, probably 90 per cent of the longleaf pine type burned over at least once every 3 to 4 years. It is extremely doubtful if a single acre of longleaf pine timber has ever grown to maturity without having been exposed to fire at least once.

In spite of the numerous fires, however, throughout the region there occur vast stands of second-growth longleaf pine. Widespread observations by foresters and numerous scientific field experiments have shown conclusively that longleaf pine, even when in the seedling state, tolerates fire to a degree unequalled by any other indigenous tree species. Pine species associated with longleaf pine are all much less tolerant of fires, especially during the juvenile stages; and it is doubtless to this difference in tolerance of fire that the thousands of acres of pure longleaf pine owe their existence.

During the past 10 years a great change has taken place in the south with respect to woods fires. With the development of region-wide interest in

¹ The publication of the extra illustrations which accompany this article has been made possible by funds other than those of the Ecological Society of America.

² The accumulation of inflammable debris, consisting of litter, herbaceous vegetation, and underbrush, in the south is called "rough."

forestry, millions of acres of land, heretofore burned over frequently, have been placed under complete fire protection. Field observations on these areas have revealed that various species of hardwoods frequently invade the pine forest. Inasmuch as hardwoods are commonly of infrequent occurrence in longleaf pine forests subjected to recurrent fires, it is apparent that fire is a highly important factor in determining composition as well as other characteristics of longleaf pine forests. As early as 1888, Miss Long stated that . . . "but for the continual annual wood firing that prevails so generally throughout the South, the Maritime Pine Belt would soon disappear and give place to a jungle of hardwood and deciduous trees." Harper ('11, '13, '14) supported this view and stated ('14) that, whereas "a fire every year during the lifetime of the tree would be likely to prevent its reproduction . . . if fire were withheld too long the oaks and other hardwoods which grow in the longleaf pine regions would take possession of the ground and gradually crowd the pine out." Chapman ('26) points out that on areas in Louisiana protected from fire for several years longleaf pine fails to reproduce itself, whereas various hardwood species quickly develop into a dense underbrush.

Most foresters in the south have long been reluctant to accept these views; however, although no data disproving the theory that the longleaf pine type is a fire climax have been published. The general attitude regarding this theory is reflected by Howe ('13), who stated that if the longleaf pine region is an exception to the old idea that unrestricted fires are disastrous to the best silvicultural conditions, the fact remains to be proved by statistical data.

It is the purpose of the present paper, therefore, to discuss the development of certain changes in stand composition of longleaf pine forests brought about by the exclusion of fire.

PRESENT STUDY

During the course of a study on the effects of fire in the longleaf pine region made by the Southern Forest Experiment Station, 51 stands of longleaf and slash pine, *P. caribaea* More., were examined.³ Each stand had been protected from fire for at least 10 years. These study areas were widely distributed within the Coastal Plain from South Carolina through the intervening states to Louisiana. In the majority of cases, immediately adjoining the unburned area was an area subjected to periodic fires. The data presented here were selected to represent several typical conditions of sites easily recognizable throughout the region.

Field conditions in longleaf pine forests. Longleaf pine typically grows in open stands. Although a normally stocked 20-year-old stand with a site index of 70 feet has per acre 1,150 trees 2 inches or more in diameter at breast height, according to the United States Forest Service ('12), the average

³ Since the completion of the field work on which the present study is based, observations, which fully corroborate the results presented here, were made on at least 50 additional long-unburned pine stands.

stocking falls far short of this. One of the characteristics of stands of second growth longleaf is understocking. Throughout most of the longleaf pine area, underbrush is practically nonexistent, there being instead a luxuriant growth of herbaceous plants, chief of which are various perennial grasses. On sandy soils of the Georgia and Florida flatwoods, however, occurs a low growth 1 to 2.5 feet high of gallberry, *Ilex glabra* (L.) A. Gray, or saw palmetto, *Serenoa serrulata* (Michx.) Hook. Understocked stands and the inconspicuous part occupied by underbrush in longleaf pine forests is doubtless largely due to the past occurrence of frequent fires.

Relation of fire to longleaf pine. Because of the open nature of most longleaf pine stands, and because of the absence of heavy underbrush, fires in longleaf pine forests are rarely of the spectacular, catastrophic type. Rather, they are generally of the surface-fire class, their chief fuel being the dense, herbaceous ground cover. In dangerous fire weather, however, these surface fires generate great heat and may cause much damage to mature timber as well as to the second growth, particularly if the rough has been accumulating for several years.

Under conditions attending most forest fires in longleaf pine forests mortality is rarely high. It is beyond the scope of the present paper to discuss the general effect of fire on longleaf pine, but a few points should be made clear. The remarkable resistance of this tree to fire has already been mentioned. Trees scorched so severely by a late winter fire that every needle is brown usually put forth new spring growth a few weeks after the fire, and within six weeks it is difficult to realize that a fire had in any way damaged the timber. No doubt the dense tufts of long needles surrounding each bud effectively insulate the bud from heat. In spite of its high degree of fire tolerance, however, under certain conditions longleaf pine is killed outright by fire. In the first place, severe fires burning through dense stands may crown in spots, in which event mortality is usually high. Fires occurring during the growing season may also exact a considerable toll. Lastly, regardless of site or other conditions, longleaf pines pass through two short and distinct periods during which they are particularly susceptible to fire. The first of these is the year following germination, when fires may completely destroy a young seedling stand. The second danger period is during height elongation, when the young tree is approximately 18 inches tall. This is a dangerous period because the maximum air temperatures during fires occur at approximately 18 inches above the ground, which roughly coincides with the height a few inches above the tallest ground cover serving as fuel. After the seedling has lived through the second of these critical stages, its chances of escaping destruction by subsequent fires are greatly enhanced.

As compared with longleaf pine, the associated tree species are very intolerant of fire, although slash pine is surprisingly resistant to fire after passing through the seedling stage. The remaining associates such as loblolly pine,

P. taeda L., and various hardwoods are generally highly susceptible to fire, with certain exceptions to be discussed later.

From the above considerations, it is not surprising that longleaf pine forests subjected to repeated fires differ greatly in stand composition from forests long protected from fire.

STAND COMPOSITION OF BURNED AND UNBURNED LONGLEAF PINE FORESTS

Longleaf pine forests subjected to recurrent fires are practically always free from hardwoods in sufficient number to be considered by the silviculturist, although occasionally a few hardwoods will persist even on areas burned over annually if the groundcover is sparse and the fires therefore are of low local intensity. Throughout the region as a whole, however, the high percentage of longleaf pine in longleaf pine types⁴ is generally recognized.

When fires are excluded from longleaf pine forests, changes in the nature of the forest soon occur, depending upon the nature of the soil. Soils of the longleaf pine region are of three general classes. These classes as shown by Bennett ('21) are: (1) well-drained sandy soils, (2) poorly drained soils of the flatwoods, and (3) the well-drained sandy loams or fine sandy loams of the Upper Coastal Plain. These divisions are important, inasmuch as the hardwood associates of longleaf pine differ for each division, and their reaction to fire is likewise different. Each of these three divisions will be discussed in order.

Well-drained sandy lands. Approximately 11 per cent of the longleaf type occurs on well-drained sandy soils. These areas are called "oak ridges" because they are somewhat higher in elevation than the surrounding topography and because one or more species of oaks is invariably present. The most abundant of these oaks, locally called scrub oaks, are blackjack oak, *Quercus marilandica* Muench., post oak, *Q. stellata margarctta* (Ashe) Sarg., turkey oak, *Q. catesbaei* Michx., blue jack oak, *Q. cinerea* Michx., and various forms of southern red oak, *Q. rubra* L. Several other species of oaks and other hardwoods occur on these dry sandy soils but are not silviculturally important.

The scrub oaks (fig. 1) are of particular interest from a forest-management viewpoint inasmuch as they are entirely distinct from other hardwoods to be considered in this paper. In the first place, if once well established, even frequent fires fail to remove them from the forest stand, owing to their ability to send out vigorous sprouts when the main stem is killed by fire. When scrub oaks attain a diameter at breast height of approximately 8 inches, their ability to sprout is much less than during earlier stages of growth. For this reason fires may kill the older oaks, whereas they simply cause an increase in number of stems per acre in younger age-classes.

⁴ Foresters generally consider a forest type a "pure type" if the dominant stand consists of 80 per cent or more of any one species. Longleaf pine forests are frequently 100 per cent longleaf.



FIG. 1. Typical "oak ridge" on deep sandy soil in Florida. The most abundant tree is turkey oak.

Since many hardwoods, principally scrub oaks, are already present on practically all of the well-drained sandy sites in the longleaf pine region, exclusion of fires from these sites does not materially affect stand composition. These dry sandy sites, therefore, constitute the sole exception to the statement made above that fire protection results in an increase of hardwoods. On these dry sites, however, protection from fire enables the hardwoods to develop much more rapidly than they would if subjected to frequent fires. For the remainder of the longleaf pine type (89%) conditions are vastly different.

Poorly drained soils of the flatwoods. Approximately 20 per cent of the longleaf pine type occurs on poorly drained soils of the flatwoods of Georgia and Florida. On practically all of these soils, most of the reproduction on areas afforded fire protection is slash pine. When dense young stands of either longleaf or slash pine occur, hardwood invasion is slow until the pine stand attains a height of at least 40 to 50 feet and the crown canopy begins to open up somewhat. This is an important qualifying statement, inasmuch as there are several million acres of land restocking naturally with dense slash and longleaf pines. Within these dense stands, hardwood invasion will probably be of little importance for 15 or more years; the length of time before invasion assumes importance will vary greatly according to site quality. Table I affords an example of hardwood establishment under a dense second-growth, mixed pine stand. The pines, which were approximately 45 years old, seeded

TABLE I. Stand table showing number of trees per acre on a longleaf pine site in flatwoods protected from fire for 20 years. Lake City, Florida¹

D.B.H. inches	Longleaf pine	Slash pine	Loblolly pine	Wax myrtle	Laurel oak	Water oak	Live oak	Red gum	Wild plum	Red cedar
1			2	168	4					
2			2	64	12					2
3				18	18		2		6	
4				18	16	2				
6	4	4	2	12				2		
8	4	14	6							
10	6	6	26							
12		6	16							
14		10	10							
16		4	8							
18			10							
20			6							
Total:	14	44	88	280	50	2	2	2	6	2
Reproduction:				80	20					

¹ The immediately adjoining forest land was 100 per cent mixed pines except around the edges of ponds, where wax myrtle, water oak, laurel oak, and red gum occurred. In this and the following tables, the designation "longleaf pine site" refers to areas that, judging from the surrounding forest types, originally grew pure stands of longleaf pine.

in an old field that undoubtedly was free from fire for several years afterwards, as attested by the presence of numerous loblolly and slash pines. After this time it was apparently subjected to recurrent fires, which evidently were not sufficiently intense to remove these species. The last fire occurred between 12 and 15 years ago, and hardwood invasion began immediately.⁵ Wax myrtle, *Myrica cerifera* L., occurred in clumps with 5 to 15 stems up to 20 feet high. Laurel oak, *Q. laurifolia* Michx., was present as a thrifty, rapidly growing tree up to 30 feet or more in height.

The most important change now occurring in the longleaf pine flatwoods

TABLE II. Stand table showing number of trees per acre on a longleaf pine site unburned for 12 years in the flatwoods, Gainesville, Florida¹

D.B.H. inches	Longleaf pine	Slash pine	Water oak	Wax myrtle	Red gum	Gallberry
1			630	770	20	
2			435	45	5	
3		5	45			
4	20				20	
6	25	15				
8	25	5				
10	40	30				
12	20	30				
14	15	5				
16		5				
Total:	145	95	1110	815	45	
Reproduction:			125	1150	100	425

¹ The adjoining forest land subjected to annual fires was 100% longleaf pine.

⁵ This statement of the owner of the private property agreed with the age of the hardwoods.

is the invasion of hardwoods on rough lands, as distinguished from abandoned cultivated land. An example of this is afforded by the following tables. Table II was made in a 35-year-old stand of mixed longleaf and slash pines, the density of which was practically normal. The last fire occurred in 1935. Water oak, *Q. nigra* L., and red gum, *Liquidamber styraciflua* L., ranging in height up to 25 feet or more, were the most important elements of the hardwood component. An idea of the great density of the stand of water oak may be obtained from figures 2 and 3, and table II, where it is seen that this tree

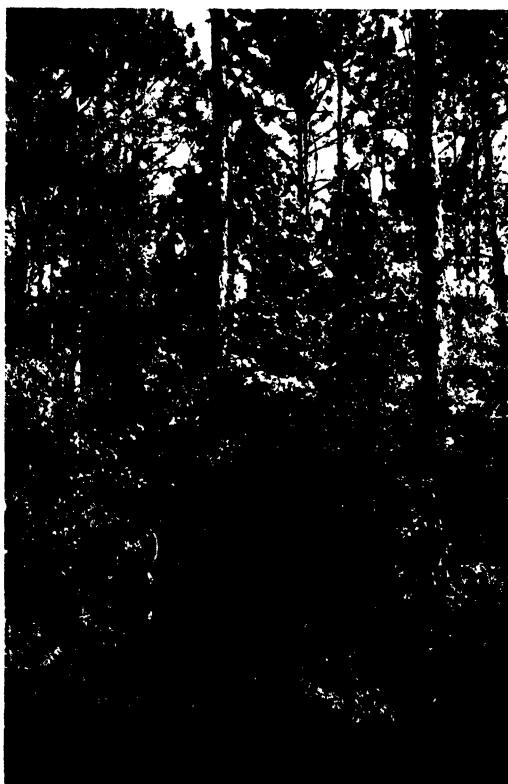


FIG. 2. A second growth longleaf-slash pine stand protected from fire for 12 years. The hardwood understory consists largely of water oak, red gum, and wax myrtle.

occurred, in spots at least, at a rate of 1,110 stems per acre. Under the dense understory of hardwoods, it was not surprising that reproduction of only the shade-tolerant hardwoods was present.

Obviously, a highly important problem in the culture of pine stands from which fire is excluded is the ultimate development of the hardwood understory. Tables III and IV are particularly valuable in exhibiting the trend of this development.



FIG. 3. Detail of the hardwood understory shown in figure 2. There were 1,110 water oaks per acre at least 1 inch D.B.H. on the plot photographed (table II).

The data for one part of table III were collected in a stand in which only one fire had occurred during a period of 25 to 30 years. This fire was of insufficient intensity to influence stand composition and apparently burned only a portion of the area. The data in the remainder of table III are from a tally in an adjacent longleaf pine stand subjected to recurrent fires every 2 to 3 years. Burned and unburned stands were separated by a woods road 8

TABLE III. *Stand tables showing number of trees per acre on a longleaf pine site in the flatwoods (I and III) unburned for 30 years and (II) an adjoining site exposed to repeated fires, Chiefland, Florida*

D.B.H. inches	Laurel oak	I Unburned Live oak	Water oak	II Burned Longleaf pine	Longleaf pine	III Unburned Laurel oak	Live oak
1						4	
2		1		6	30		
3	4	6		6	46	22	
4	11	1		68	34	38	2
6	15	1	3	98	44	24	
8	15	2		104	12	30	
10	17			34		2	
12	6			4		2	
14	7					2	
16	1						
18	1						
Total	77	11	3	320	166	124	2

feet wide. Although the pine in that portion of the 40-acre unburned tract immediately adjoining the burned stand had been logged a few months before the stand table was prepared, this has no bearing on the important point shown in this table, namely, the abundance of sizable oaks in the protected stand in contrast with the complete absence of oaks or other hardwoods in the burned stand (fig. 4).



FIG. 4. Longleaf pine in Florida flatwoods protected from fire for 30 years (A). Note the abundance of laurel oak (table III). Similar and adjacent to this is a stand of longleaf pine with hardwoods completely excluded by fire (B).

Table IV, based on a longleaf pine forest unburned for probably 75 years or more, affords even more definite information regarding the ultimate development of the hardwoods (fig. 5). Within this stand of virgin pine the hardwoods formed an important component. In the first place, little or no pine reproduction occurred, practically all the reproduction more than 1 year old being wax myrtle; this was not tallied in the stand table. Laurel oak seedlings less than 1 year old were numerous in spots, but even if these survive the dense shade, their development beyond a suppressed stage would be unlikely, inasmuch as the crown canopy was practically closed. Wax myrtle, red bay, *Persea borbonia* (L.) Spreng., holly, *I. opaca* Ait., sweetleaf, *Sym-*

TABLE IV. Stand table showing number of trees per acre on a virgin longleaf pine site unburned for 75 years in flatwoods, Cumberland Island, Georgia

D.B.H. inches	Longleaf pine	Laurel oak	Live oak	Chapman oak	Red bay	Wax myrtle	Christmas holly
1					12	103	
2	1			5	29	27	4
4	5			3	38	1	3
6	6				9		
8	2				3		
10	1		1		3		
12	5		3		1		
14	5	1	1				
16	10						
18	7						
20	10	1					
22	7	3					
24	4	1					
26		1					
28	1	1					
30	1						
Total	65	8	5	8	95	131	7



FIG. 5. Virgin longleaf pine protected from fire for 75 years or more (table IV), with dense hardwood understory and many wolf trees, laurel and live oaks. Cumberland, Ga.

plocus tinctoria (L.) L'Her., and tree huckleberry, *Vaccinium arboreum* Harsh., formed a conspicuous understory of widely varying density up to 25 feet high. Sweetleaf and tree huckleberry, although absent from the plots on which the stand table was based, were common in other portions of the stand. The development of the laurel and live oaks is best seen from figure 6. Thirteen of these "wolf" trees per acre occurred on the plots examined in detail, as compared with 51 longleaf pine 10 inches D.B.H. or

over. The largest of these wolf trees occupied approximately 4 times the crown area of a mature longleaf pine 150 to 200 years old. Although the data at hand are inadequate for a reliable estimate, the statement that within certain portions of the stand 30 per cent of the canopy of the high forest was occupied by laurel and live oaks is probably conservative. The understory

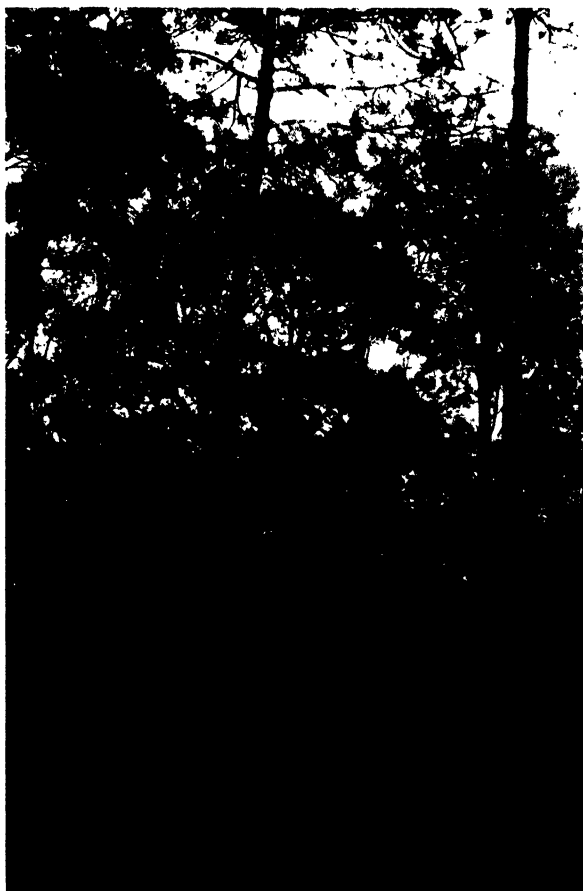


FIG. 6. Longleaf pine with dense understory of oak due to protection from fire for 75 years or more.

was practically 100 per cent hardwoods, the species of which have already been mentioned.

The Upper Coastal Plain. Approximately 69 per cent of the longleaf pine type occurs within the Upper Coastal Plain, the heavier textured soils of which afford some of the finest sites for longleaf pine. Moreover, these sites support a wider variety of hardwood species than the more sandy soils of the flatwoods.

TABLE V. *Stand tables showing number of trees per acre for second-growth longleaf pine unburned for 25 years and for an adjoining stand burned annually on a moist site in the Upper Coastal Plain, Summerville, S. C.*

D.B.H. inches	Long- leaf pine	Lob- lolly pine	Black gum	Red gum	Red maple	Wax myrtle	Laurel oak	Black- jack oak	South- ern red oak	Water oak	Sweet bay	Christ- mas holly	Su- mach
<i>Unburned for 25 years</i>													
1	15	42	22	15	5	8	12				10		
2	38	40	18	3				2	2				
3	52	25	5					2					
4	62	10	10										
6	120	12	5										
8	107												
10	67	2											
12	18												
14	2	**											
Total:	481	131	50	18	5	8	12	4	2		10		
Reprod.:	12	70	18	12	8	10	2			2	18	2	5
<i>Burned annually</i>													
1	7												
2	58												
3	38												
4	65							2					
6	113												
8	67							2					
10	39												
12	2												
14	2												
Total:	381							4					
Reprod.:	12										1		

TABLE VI. *Stand table showing number of trees per acre for culled-over old-growth longleaf pine on a well-drained site in the Upper Coastal Plain, unburned for 12-15 years. Vicinity of Flomaton, Alabama*¹

D.B.H. inches	Longleaf pine	Flowering dogwood	Post oak	Southern red oak	Sassafras	Black gum	Sweetleaf
1-2		420	250	140		30	10
2-4		280					
6							
8	10						
10							
12							
14	20						
16	10						
18	10						
20	10						
22	10						
24	10						
Total:	80	700	250	140		30	10
Reproduction:		360	140	30	20		

¹ No hardwoods present in adjoining longleaf pine forest exposed to frequent fires

In general, hardwood development on areas protected from fire progresses along similar lines in both the Upper Coastal Plain and the flatwoods, the chief difference being in the species of hardwoods. Within the Upper Coastal Plain dogwood, *Cornus florida* L., southern red oak, red gum, and



FIG. 7. Old-growth of longleaf pine in the Upper Coastal Plain, unburned for 12-15 years (table VI). Note abundant understory of hardwoods (A). Old-growth longleaf pine separated from (A) by a creek and subjected to repeated fires (B).

black gum, *Nyssa sylvatica* Marsh., are generally abundant, the dogwood and southern red oak prevailing on the well drained sites and the gums on the moister sites. Stand conditions for these two general sites are shown in tables V and VI.

The wide variety of hardwoods typical of moist longleaf pine sites is shown in table V, although on the unburned plot on which this table was

based, red gum was much less abundant than is typical for unburned forests on comparable sites. The burned and unburned timber stands represented by table V were separated by a firebreak 4 feet wide.

The heavy stocking of dogwood, post oaks, and southern red oaks on better drained sites protected from fire is shown in table VI and also in figure 7A.

No area in this portion of the longleaf pine type having a greater period of protection than the areas represented in the preceding tables was available for study. For this reason it is not possible to follow through the ultimate development of the hardwoods; but a few further observations and comments are worthy of attention. Dogwood, because it rarely exceeds a height of 25 feet at maturity, will unquestionably always remain a subordinate species with respect to crown classification. On the other hand, there is good reason to believe that southern red oak and post oak will continue to develop until they occupy positions as dominant and codominant trees in the pine stand, thus creating a mixed pine-hardwood stand. The best evidence supporting this statement is furnished by the fine mixed pine-hardwood forests of Arkansas, where southern red oak and post oak occur as dominant trees with loblolly, *P. taeda* L., and shortleaf pines, *P. echinata* Mill.

The future of red and black gums is not entirely clear because of limited study areas on which trees more than 25 years old occur. From their present rates of growth, however, it seems apparent that these trees will also ultimately work their way into the same crown class as that of the pine overstory.

GENERAL DISCUSSION

An important factor influencing the rate of the hardwood invasion following fire protection is the source of seed supply, which field observation shows to be particularly important within the Inner and Upper Coastal Plains. In these portions of the longleaf pine region, certain large forest properties protected from fire for 10 years have no appreciable hardwood undergrowth. Although exceptional, these areas are sufficiently extensive to be noteworthy. While the dense, even-aged stand of longleaf pine has unquestionably been a potent factor in checking the establishment of hardwoods, probably of equal importance is the dearth of hardwood seedtrees. The rolling country is in general well drained along definite stream courses, and only around these drainage courses are hardwoods to be found. Although these consist largely of sweet bay, *Magnolia virginiana* L., and swamp black gum, *Nyssa biflora* Walt., neither of which is aggressive nor appears to grow well on sites occupied by longleaf pine, observations made elsewhere in the region indicate that more aggressive hardwoods will eventually invade these pine forests, with birds and rodents playing an important role in the dissemination of seed.

From the foregoing data it is evident that exclusion of fire from long-

leaf pine forests will ultimately result in an invasion of hardwoods, chiefly oaks and red gum. Where hardwoods become established under a stand of pine at least 25 to 30 years old, no particular silvicultural problem is presented until the pine has been harvested. When the pine is to be removed, however, it will be necessary to consider all possible means of subduing or eliminating the hardwoods until adequate pine reproduction has been obtained.

Unless preventive measures are taken, a pronounced change from pure pine to mixed pine-hardwood forest will eventually become evident, following fire protection. Of the considerable number of hardwood species comprising the group of aggressive invaders within pine forests, only two seem capable of ever attaining commercial value—dogwood and southern red oak. Dogwood, which has a number of specialized uses, brings a good price if sufficiently abundant, while southern red oak is held in high esteem by the lumber industry. It seems extremely doubtful, however, whether sufficient quantities of these trees to be profitable would ever develop naturally within longleaf pine forests. The commercial future of second-growth black and red gums, on longleaf pine sites, is doubtful. These trees are valuable only if of high quality, and inasmuch as they are bottomland species they are not likely to develop to merchantable size where associated with longleaf pine. Lastly, the laurel and live oaks, which develop so rapidly in the flatwoods when afforded fire protection, are at the present time entirely unmerchantable. Because of the high utility of pines and the negligible demand for the hardwoods discussed, it is therefore apparent that hardwoods, *from a timber-production standpoint*, have no place in a management plan for longleaf or slash pine forests.

Although the majority of the unburned forests were longleaf pine, the identical ecological trends found in longleaf forests apply equally well to slash pine. In fact, the slash pine reproduction which occurs so extensively throughout former longleaf pine sites in Georgia and Florida largely originates from trees around ponds. These moist sites, largely protected from fires in past years by the presence of standing water, are also occupied by moist-site hardwoods such as water and laurel oaks, red gum, black gum, and red maple. As has been already pointed out, red gum and especially water and laurel oaks are exceedingly aggressive in spreading to adjoining sites protected from fire. These species, therefore, appear destined in the future to invade slash pine stands in varying numbers unless some measure is taken to prevent their doing so.

A point entirely distinct from the merchantable value of the hardwood invaders is the value of these trees in *building up soils* of longleaf or slash pine forests. The use of hardwoods mixed with conifers for soil building purposes is a common practice in European countries. Hesselman ('25) states that, in southern Germany, a stem count of 10 per cent beech is desired in coniferous forests to prevent an unfavorable humus condition. In north-eastern United States the desirable mull forms of humus are generally asso-

ciated with the occurrence of hardwoods. However, a recent study ('36) has revealed that raw humus⁶ formation is not found in the longleaf pine region regardless of stand composition. It should also be pointed out that on soils extremely low in plant nutrients and of high acidity, longleaf and slash pines commonly make annual height growths of 2.5 to 3 feet, provided soil moisture conditions are favorable. It appears, consequently, that lack of moisture and not lack of nutrients is the factor limiting growth. Furthermore, although dogwood is recognized as an excellent soil builder, oaks may be of little or no value for this purpose; it is even probable that certain species of oak, among which are laurel and live oaks, are actually detrimental to the soil. Red and black gums with their readily decomposable leaves, however, would doubtless be of some benefit to the soil. The presence of a hardwood component in longleaf pine forests, therefore, has little justification from a soil building standpoint.

A further consideration which must be given to the invasion of pine forests by hardwoods is their relation to *game management*. Pure coniferous forests, particularly when dense enough to afford a closed crown canopy, are an undesirable habitat for wild game in the region being discussed, owing to the fact that available food is restricted in variety and also, during poor seed years, in quantity. In unburned forests such as those described above, it is likely that wild turkey and deer would find a variety of food not available on frequently burned lands.

On the other hand from the standpoint of game management a diversity of ecological conditions is always desirable. Areas of pure longleaf pine in which are interspersed areas of mixed hardwoods and pine are preferred to vast unbroken areas of either as a pure type. Inasmuch as the longleaf pine region already contains from 10 to 30 per cent hardwood types in the form of swamps and "ponds," an increase in the number of hardwoods in the region has only small significance with respect to improving game management.

Although food supply is of paramount importance in game management, it is by no means the sole consideration. The problem of parasites as shown by Stoddard ('35) in unburned forests is another factor to be considered; and it has been pointed out by game specialists that fire protection appears to favor the development of redbugs, ticks, and other parasites.

METHODS OF CONTROLLING STAND COMPOSITION

Removal from the stand of undesirable hardwoods is by no means a new problem to foresters. In most forest sections east of the Mississippi River, as well as in Louisiana, Arkansas, and Texas, it has been found desirable to attempt the removal of less desirable species in the management of those more

⁶ In cool climates a forest floor sometimes a foot deep develops under pure stands, usually conifers. Even where this excessive accumulation does not occur, the organic matter is matted together in a tough, poorly aerated layer. The humus layer found under these undesirable conditions is called raw humus.*

desirable. Although various methods of girdling and poisoning have been resorted to with varying degrees of success, the cost of these treatments per acre is high. Removal of the hardwood during the first thinning would appear to solve the problem practically, but inasmuch as most young hardwoods sprout prolifically following cutting, their removal would be largely temporary. Within the longleaf pine region, an additional treatment that seems feasible is the use of controlled fires. Silviculturists familiar with longleaf and slash pines realize that after either of these species has attained a height of 15 feet it is entirely possible to pass a controlled fire beneath the pine stand without materially affecting growth or causing appreciable mortality. Hardwoods, however, are so much less tolerant of fire than are pines, that practically all hardwoods smaller than 2 inches D.B.H. are killed by the controlled fire. Therefore, on areas well stocked with pines large enough to permit controlled burning, invasion of new hardwoods would appear to be manageable by this method. On the other hand, in stands in which the hardwoods and pines were established simultaneously and where fires hot enough to kill the hardwoods would also seriously damage the pines, removal of the hardwoods during thinning operations seems to be the logical solution. On these areas, however, a controlled fire 2 to 4 years after the thinning would probably hold the hardwoods in check by killing the sprouts.

SUMMARY

A detailed study was made of stand composition of 51 long-unburned forests of longleaf and slash pines as compared with nearby forests subjected to repeated forest fires. The areas studied were widely distributed over the longleaf pine region from South Carolina to Louisiana.

Hardwoods were numerous in practically all longleaf pine stands of pole size or larger from which fires had been excluded for more than 10 years. In dense young pine stands hardwoods were not present in sufficient number to present a problem. The study revealed a strong trend toward hardwood invasion in such stands, however, the hardwoods becoming increasingly abundant as the pines increased in height, since the increased space beneath the pine canopy gave more room in which the tolerant hardwoods might develop. On areas where no fires had hindered the growth of the hardwoods, they had developed into dominant and codominant trees in the pine stand and occupied a considerable percentage of the total crown space within the dominant stand.

As a direct result of fire protection, therefore, a pure longleaf pine type may become a mixed pine-hardwood forest. Furthermore, if no silvicultural measures are taken to retard the development of the hardwoods, it seems evident that pines will ultimately be completely excluded from the forest by hardwoods. This conclusion is in accordance with previous ideas expressed in the literature as early as 50 years ago.

Inasmuch as the hardwoods which invade the pine forests have less commercial value than the pines, and, whereas there appears to be no important

reason for retaining these trees in the stand for soil building, the hardwoods have no place in a forest-management plan for either longleaf or slash pine. From the standpoint of game management, however, because of their value as a source of a variety of foods, retention of these species on small scattered spots of a few acres each may be desirable in certain localities where hardwoods are now generally absent.

If hardwoods are not desired in a particular stand of pine, it may be possible by use of controlled fires to prevent their invasion. If the hardwoods are already present, however, and are above 2 inches in diameter, it is suggested that they be removed during a thinning operation and that the sprouts developing after thinning be kept in check by controlled burning.

It is not intended in this paper to show that fire protection will uniformly cause undesirable ecological changes in stand composition throughout the longleaf pine type. Rather, it is desired to stress the idea that the silviculturist should be alert in observing these ecological trends, the interruption or encouragement of which will depend not only upon the intensity of their manifestation but also upon the management plan of the particular forest in question.

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REVIEWS

THE EVOLUTION OF SOCIALITY ¹

This book embodies a series of Norman Wait Harris lectures at Northwestern University, that gave the author the opportunity and stimulus to bring together in ordered form his mature conclusions and judgments regarding sociality and the precursors of sociality in the lower animals. The result is notable, and in every respect worthy of the deservedly high repute of the author. He has once more put all biologists heavily in his debt for a clear and logical account of a field of research that has in the past too often been the playground of pseudophilosophers, whose knowledge of biology was even more fractionally-baked than their sociologic ideas.

Virtue has been made of the necessity imposed by a public lectureship to state what was to be said in simple language that would convey its meaning to any literate person of moderate intelligence. The direct and charming simplicity and clarity of the platform delivery has been carried over into the printed book. Prof. Allee explains with great cogency why this is a virtue (pp. 17-18) :

Despite much practice to the contrary, any biological fact which concerns us can be accurately described and the conclusions from its study be clearly expressed in relatively simple and direct language. In research reports and scholarly discussions there is need for the conciseness and precision made possible by technical language. Science has no need, however, and is ill-served by any tendency to develop a cult of obscurity. Scientists must be free to attack the unknown as effectively as they can and in return for intellectual freedom they have an obligation, which rests heavily on those able to do so, to interpret research results in terms which can be understood by intelligent and interested people.

This statement should be a stimulus to youngsters beginning their professional careers, urging them on to take some real pains to learn how to write; and at the same time a shaming rebuke to those oldsters who, themselves quite unable to write a paragraph that anyone would conceivably ever read except under dire compulsion, make it their business to sneer at any exercise, by a scientific man of a literary competence that surpasses their own.

Prof. Allee begins his treatment with a review, so brief as to be somewhat less than entirely adequate, of the history of ideas about the development of primitive sociality among animals through cooperation and "mutual aid," from Empedocles to William Patten, noting along the way the position and contributions (if any) of Anthony Cooper the third Earl of Shaftesbury,

¹ **Allee, W. L.** 1938. *The Social Life of Animals.* W. W. Norton and Co., New York. Pp. 293. Price \$3.00.

Espinas, Prince Kropotkin, Deegeneer, and Alverdes. This historical introduction is followed by a rapid sweep of the eye over some of the more conspicuous examples of animal aggregations from the invertebrates to the mammals, leading to the statement (p. 49) that:

The conclusion seems inescapable that the more closely-knit societies arose from some sort of simple aggregation, frequently, but not necessarily, solely of the sexual-familial pattern. Such an evolution could come about most readily with the existence of an underlying pervasive element of unconscious co-operation, or automatic tendency toward mutual aid among animals. In the simpler aggregations evidence for the presence of such co-operation comes from the demonstration of survival values for the group. These are more impressive the more constant they are found to be. If they exist throughout the year they are much more important as social forerunners than if present only during the mating season or at times of hibernation.

Chapter III and the major portion of Chapter IV present a masterly review of the experimental evidence that biologically optimal population densities are not necessarily minimal densities—that in other words a certain degree of crowding of organisms is often beneficial, as judged by rates or outcomes of various physiological processes. Much of this evidence has, of course, come from the careful, thorough, and critical investigations of Allee himself and his students. The results that have accrued from these population density studies, and they now include a wide range of animal forms, and have been discovered and worked out by a considerable number of different independent workers, are held (p. 50) to be “evidence for the assertion that there is a general principle of automatic co-operation which is one of the fundamental biological principles.” This way of putting the matter, which is in fact in some sense the central thesis of the book, will inevitably lead to discussion. Does the mere fact that n animals survive longer in an unfavorable solution than do $n + m$ or $n - m$ animals in itself demonstrate that there is any element of true cooperation, automatic or otherwise, between the individuals to bring about the achievement of the favorable result? Is not further evidence, and of a qualitatively different sort, necessary to prove such a conclusion? There is an absolutely ineluctable element of teleology in such words as “cooperation” and “mutual aid” which make them not quite good and reliable servants for purely descriptive—which is to say exclusively scientific—purposes. It would seem that the sort of observed biological effects of population density here under discussion do not, in cold logic, warrant conclusions about cooperation as a fundamental biological principle. The actually observed phenomena appear to be of the same sort and order *logically* as many that are confined to purely chemical levels. For example, consider the following well-known facts: if we remove a part, say 10 per cent, of the water in which the conversion of ammonium cyanate into urea is taking place, and bring the solution up to its original volume by adding acetone, *which takes no part in the reaction*, the rate of the conversion increases by nearly 50 per cent. Similarly in ethyl alcohol the rate of transformation of the cyanate into

urea is thirty times as great as it is in pure water, other conditions remaining the same.

The result in this chemical case turns upon the proportionate numbers of molecules and ions of the different sorts, per unit volume of universe, just as in the animal density-of-population cases the outcome depends upon the numbers of organisms per unit volume of universe. But who would ever think of suggesting that any of the molecules or ions concerned "cooperated" with each other or with anything else to produce the quantitatively different result got when either acetone or alcohol was replacing a part of the water; or that acetone and ammonium cyanate "mutually aided" each other? Until a great deal more is known than now is about the detailed steps in the causation of the observed biological results of which we are speaking, are we justified in thinking of cooperation, or anything whatsoever of the nature of sociality, as being involved in the case? The question is raised here not so much as a criticism of the position taken by Allee, but rather to emphasize the extraordinary epistemological difficulties that inhere in any attempt to trace and *prove* the beginning stages in the evolution of sociality.

In Chapter V group behavior is discussed, and in particular work on the influence of numbers of organisms together upon rate of learning is summarized. In general the evidence indicates that even far down in the evolutionary scale the numbers of organisms present together affect individual behavior both quantitatively and qualitatively. To be absolutely precise about the matter, what the observations demonstrate (and all that they demonstrate) is a statistical association between differences in numbers of organisms present and differences in behavior. Allee regards such facts as *per se* evidence of the existence of social behavior. He says (pp. 173-4):

Reactions may be regarded as social in nature to the extent that they differ from those that would be given if the animals were alone. From this point of view social behavior may have or may lack positive survival value. All that is necessary is that the behavior be different from that which would be given if the animal were solitary. In this sense all the animals whose behavior we have been discussing are social to a considerable degree: the more so, the greater the difference between their behavior when grouped and when isolated. When the behavior of such animals as cockroaches, fishes, birds and rats shows evidence of distinct modification as a result of more than one being present, we have another suggestion that there exists a broad substratum of partially social behavior. There are many indications that this extends through the whole animal kingdom. From such a substratum, given suitable conditions, societies emerge now and again as they have among ants and men. At these higher social levels, as is to be expected, the type of behavior shown under many conditions is related even more closely to the number of animals present than with less social cockroaches and fish.

Here again opinions are likely to differ on the point of interpretation. The number of individuals present together in a limited universe mechanically and necessarily in some degree conditions and determines the behavior of each individual in the aggregate, whether the individuals are inanimate marbles, or are living mice or men. Is there justification for concluding, because dif-

ferences of behavior are associated with differing numbers involved, that the behavior has therefore become *social*? Because it is much more difficult in the ancient *Pigs in Clover* game to corral the little balls (pigs) in the pen when there are several of them than it is when there is only one, probably does not mean that we are justified in thinking that when there are, for example, four balls their behavior has suddenly become social and represents organized community resistance to the despotism of the ogreish human player who is trying to coerce them all into the little central pen.

Chapter VI deals with group organization as observed in small flocks of birds of various sorts. The discussion is again based largely upon the work of Allee and his own students, and is extraordinarily interesting and instructive. Here we are dealing with behavior patterns that are unquestionably at the level of primitive sociality, and generalizations begin to emerge that appear to be universally valid, such as that hierarchical social rank is nowhere necessarily or highly correlated with leadership, that highly important element in mammalian sociality.

Chapter VII under the title "Some Human Implications" treats mainly the problems presented by war, and the bearing upon them of the facts of human population density and growth. War is an indubitably tough nut for the "principle of cooperation" to crack, but Dr. Allee's optimism does not falter. It is plainly true, as he says (p. 243), that:

* There seems to be no inherent biological reason why man cannot learn to extend the principle of co-operation as fully through the field of international relations as he has already done in his more personal affairs. In addition to the unconscious evolutionary forces that play on man as well as on other animals, he has to some extent the opportunity of consciously directing his own social evolution. Unlike ants or chickens or fishes, man is not bound over to form castes or peckorders or schools, or to wait for a reshuffling of hereditary genes before he can discontinue behavior which tends toward the destruction of his species.

But the sad fact is that intelligence, reason, honesty, and decency are not the exclusive motivators of human behavior. If they were, war would have disappeared long ago. But it is still unfortunately necessary to reckon with those seven capital sins that first-flight theologians never under-rated as activators in human biology. Pride, covetousness, lust, anger, gluttony, envy, and sloth are still ranking vices, and for precisely the reason long ago alleged by the sagacious St. Thomas Aquinas—now, if wide-spread rumors are to be credited, vicariously an active, even if slightly sepulchral member of the faculty of the very university that Dr. Allee adorns. As the great Thomas pointed out, a capital vice always envisages what is, or at least is regarded as, an exceedingly desirable end; so desirable in fact that man, imperfect mammal that he is, will sin for it. It is probably a long way yet that we shall have to go on the pathway of evolution before wars happen no more.

The final chapter discusses the question: "When does an animal group become truly social?" As may have been anticipated from what has already

been said, Dr. Allee answers this query by stating a philosophical position, rather than in particulate objective terms. That position amounts to a sort of all-embracing pan-sociality, practically co-terminous with animal life itself. As he states it, pp. 274-5) :

And since no one has yet demonstrated the existence of truly asocial animals it is impossible to define the lower limits of sub-social living. All that can be found is a gradual development of social attributes, suggesting, as has been emphasized throughout this book, a substratum of social tendencies that extends throughout the entire animal kingdom. From this substratum social life rises by the cooperation of different mechanisms and with various forms of expression until it reaches its present climax in vertebrates and insects. Always it is based on phases of mass physiology and social biology which taken alone seem to be social by implication only.

This is essentially the position to which William Morton Wheeler came in his "Emergent Evolution and the Social" (1927). Indeed Wheeler, by precisely the same sort of reasoning as that which led him, and now Allee, to see universal sociality in the world of living things, pushed the concept of sociality back "to the very atom with its organization of component electrons."

Whether one regards this as a useful and important end-point to have reached would seem to depend a good deal upon the conception of sociality with which one starts. For Wheeler, in his frame of mind *at the time* of writing the little book just referred to, the concept of sociality had been reduced by a brilliant train of reasoning to complete equivalence with the concept of organization, *et practerea nihil*. What then are the consequences of such a triumph of ratiocination going to be? Well, first of all if organization means and is sociality, then truly enough all the world, animate and inanimate, *is* social, because organization is universal. But has anything been gained beyond verbalism? If we stick to reality it is plain that the clear sense of even a child is aware that the kind of mechanistic organization that characterizes a watch, for example, is, in all its meaningful aspects, wholly disparate to the kind of social organization that characterizes a symphony orchestra, and that understanding one kind is of no help at all towards understanding the other. In short, proving that one abstraction is wholly equivalent to another abstraction butters only metaphysical parsnips. Is it not evident that the very concept of sociality arose only because the human mind perceived that in the relations of some kinds of living organisms to each other and to the rest of the world there was something new and different from other sorts of experience, and something that therefore required separate conceptual establishment on its own account? Does not an all-embracing pan-sociality that includes atoms destroy all useful meaning that the concept of sociality had at the start, and leave it about as exciting as a non-alcoholic cocktail or a de-nicotinized cigar? Finally, if the argument just set forth has any cogency, would it not be about equally cogent and significant if there were to be substituted for Wheeler's "organization," each time it occurs in the argument, Allee's "automatic cooperation"?

The qualities that make this book of great significance and value are its clarity, its firm hold upon experimental reality as the only way to get a true understanding of the evolution of sociality, its modesty, and its profound intellectual integrity. It should greatly stimulate further observational and experimental research in a field where, after all, scarcely more than the surface has been scratched. Perhaps broad interpretative generalizations may wisely be left until a wider and deeper body of observational and experimental material is at hand—material of just the sort that Allee and his associates have contributed and are all the time extending.

RAYMOND PEARL

THE JOHNS HOPKINS UNIVERSITY

A NEW RUSSIAN TEXTBOOK IN ECOLOGY¹

Another milestone in the advance of ecology in the U. S. S. R. is marked by the appearance of Kashkarov's second text in this field. The title of this book is somewhat misleading since it inadequately covers the viewpoint of the author; Prof. Kashkarov, of the Leningrad State University, is a strong proponent of the biotic community (biocenosis) concept: "From our point of view, ecology is the science of the relations of organisms to the environment, the environment being not only physical but also biotic. We cannot study the distribution of organisms or of isolated species only in relation to their physical surroundings, for their environment includes the biotic environment as well. We must study all species as members of a biocenosis and must focus our attention not upon a particular species but upon the biocenosis as a whole, on the interrelations of its members, on the relations of each biocenosis as a definite unit with the conditions of the habitat."

The organization and method of presentation of his text might well serve as a model which any course in ecology could adopt profitably. In chapter 1 are presented sections dealing with the various definitions which have been given to ecology, the relations of ecology with the other sciences, the methods and points of view of ecology, an historical account of the development of ecology in the U. S. S. R. and abroad, and the significance and practical value of ecology in human economy.

The second chapter deals with "Factors of the environment and their significance in the ecology of animals and the formation of biocenoses." This is introduced by an account of the general functioning of such factors and is expanded into sections dealing with climatic, edaphic, and biotic factors. Under the first of these are considered the study of climographs, eco- and microclimates, developmental rates, etc., and under the third, biotic interrelations of which four principal types are listed: food relations between

¹ Kashkarov, D. N. 1938. Principles of the Ecology of Animals (in Russian). 602 pp. 140 fig. Moscow and Leningrad: Medgiz (State Publishing House for Medical Literature). 9 Rubles, 45 Kopecks. See also "Environment and Biocenosis," reviewed in *J. Anim. Ecol.* 2: 125. 1933.

plants and animals, predation and parasitism, the struggle for existence, and the biotic potential.

In chapter 3, "The arena of life and its subdivisions," are discussed the principles and problems involved in the various concepts of life zones and of habitats. The fourth chapter discusses the "Ecology of domestic animals and acclimitization," a field in which Kashkarov recently has been actively interested and which is developed from three principles: (1) every species, breed, stock, etc., has evolved under the selection of and hence is adapted to certain environmental conditions; (2) while a species may be adapted to a given region, other areas may be found which are likewise suitable; (3) "neither the organism (an historically formed system) nor the environment (another historically formed system) is stable: they can vary and man can modify them (by hybridization, artificial pastures, etc.)." The application of these principles is illustrated by references to his own recent work on the Kara-Kul sheep.

The next four chapters deal with the biocenosis in its various aspects, giving an introduction to the community concept, internal structure and relationships, "The structure or morphology of biocenoses and their systematics," and "The life of biocenoses in time." The latter chapter deals with the fluctuations of population numbers during the day, year, and longer periods, and with seral and historical succession. The ninth chapter considers "Trends in the investigation of biocenoses and principal aims in their investigation" and reviews much of the recent American and Russian work on community ecology, concluding with an outline of recommendations with regard to the investigation of communities. The tenth chapter is concerned with "Quantitative methods in ecology and in the investigation of biocenoses in particular" with reference to both plant and animal evaluation.

The next two chapters deal with subjects not always included in the typical text in ecology: "Adaptation (adjustment)" (from an ecological point of view) and "Ecology and evolution—the role of ecology in relation to the path of evolution." In the latter are included discussions on ecotypes, the adaptive character of evolution, the question of evolutionary biotic complexes, and a series of "other problems of ecology in the study of evolution" which is particularly interesting since they appear to have been developed independently of Elton's *Animal Ecology and Evolution*. They include the following: variation, the time of reproduction of species, migration, the struggle for existence (*sensu* Gause and Volterra), selection in nature, phylogeny, minor adaptations, isolation, and the rôle of ecological environment in paleontology.

Chapter 13 is devoted to the "Ecology of deserts as an illustration of the interrelations of the environment, the organism and their complexes" and is a good summary of the extensive studies conducted in Central Asia by Kashkarov and his associate, E. P. Korovin, since about 1924.

The final chapter on "Synecological work in the field" deals with general

points of view and practical considerations to be observed in the study of communities.

The place of ecology in a planned social economy is concisely stated in the following (which unfortunately loses much of its force in translation): "Research on the ecology and ecological interrelationships of such biocenoses having economic value as those of steppes and of the various forest types enables us to learn how to regulate and reorganize the life of these biocenoses. In addition, matters of great theoretical interest are introduced by such types of investigation, giving us an understanding of that which surrounds us in nature, its structure, and the life of natural complexes."

It is immediately apparent that the author is well acquainted with the world literature on ecology and that in this book he is making available to Russian students many of the findings of foreign workers; however the citations—both Russian and foreign—constitute by no means the only valuable features of the book: many new and thought provoking principles and ideas are expressed and it is indeed unfortunate that there is in America such a restricted reading public for it and the other Russian ecological studies which are now appearing.

J. RICHARD CARPENTER

THE UNIVERSITY OF OKLAHOMA

PRIESTLEY AND SCOTT'S INTRODUCTION TO BOTANY¹

An introductory course along the lines compassed by this text would lay, for the beginning student, a solid foundation in fact about the flowering plant, and in method of observation and use of the microscope; it would, however, introduce him to a very limited portion of the field of botanical science. The course, as to content, appears to have been determined on the supposition that those taking it will elect advanced courses, rather than as a cultural course intended to give a general survey of the science of botany for those who may not, as well as for those who may, take more advanced courses. In perusing the chapter headings one is struck at once with how much smaller a range of the subject is covered than is the case with most introductory texts in the United States. The following quotation should be of interest to ecologists:

"Whilst botanical study may . . . be sub-divided into different branches, it cannot be over-emphasized that there is only one subject of study, the plant Our study will have to stop short of any close examination of the relation of the plant to its environment or habitat. These relations are very intimate, and their analysis throws much light upon the characteristic form and functional activities of particular plants, still more upon their distribution. The studies of plant distribution, geographic botany, have of

¹ Priestley, J. H. and Lorna I. Scott. 1938. *An Introduction to Botany: With Special Reference to the Structure of the Flowering Plant.* x + 615 p. 170 figs. Longmans, Green & Co. New York. \$6.00.

recent years become associated with the study of the plant in its natural habitat—plant ecology.”

C. STUART GAGER

BROOKLYN BOTANIC GARDEN

FACTORS AFFECTING ESTABLISHMENT OF DOUGLAS FIR SEEDLINGS¹

There is wide variation in the rate and adequacy of natural restocking of cut-over and burned-over forest areas in the productive Douglas fir region of the Pacific Northwest. Mr. Isaac in his study of the effect of various physical and biotic factors on the establishment of Douglas fir seedlings has provided considerable information on the causes of success or failure of natural regeneration when a seed supply is available.

Heat injury, drought, frost and rodents appear, in about the order listed, as the major causes of seedling loss, any one of which might destroy most of a year's crop. Additional losses result from insects, competition, and mechanical injury. Newly germinated seedlings may be injured by a surface soil temperature of 123° F. or killed by a temperature of 125°. Frost injury to tender seedlings occurs at temperatures as high as 27°. It is significantly noted that the poorest seedling survivals occurred under complete exposure on cut-over land and under the full shade of the virgin forest and that the best survival occurred in well-shaded locations on cut-over land. Drought, listed second as a cause of mortality, would no doubt be first were it not that the normal drought period occurs late in the summer after many seedlings have been killed by other agents. Slash burning, in proportion to its severity, intensifies drought conditions through destruction of shade material and the removal of humus from the soil.

In general the study provides considerable basic silvical information valuable in planning ways and means of leaving Douglas fir cut-over lands in a more favorable condition for prompt natural restocking.

J. W. KIMMEY

U. S. DEPARTMENT OF AGRICULTURE

¹ Isaac, Leo A. 1938. Factors Affecting Establishment of Douglas Fir Seedlings. *U. S. Dept. Agri. Circ.* 486. 45 pp., 19 fig., 14 tables.

BOOK NOTICES

Roberts, Edith A. and H. W. Reynolds. 1938. The role of plant life in the history of Dutchess County (N. Y.). 44 p. 19 fig. 3 map. *The Authors, Vassar College, Poughkeepsie, N. Y.* After a sketch of the geologic past, with the vegetation of the various periods, the probable succession of plant communities following the retreat of the last ice sheet is outlined and the environmental factors which have affected plant life are discussed. These include climatic factors that are given in some detail. The consideration of man's influence on vegetation includes a discussion of Indian encampments at the coming of Europeans and, the location of early European settlements from 1683 onwards. Special attention is given to the location of grist and saw mills of which there were some 93 in 1797. Many details of early patents for land and of early town boundaries are given with maps. Lists of native plants and suggestions for the use of such plants for park and home planting are given together with a bibliography of 88 titles.

Muenschner, Walter C. 1939. Poisonous Plants of the United States. xvii + 266 p. 75 fig. *The Macmillan Co. New York.* \$3.50. Following a general discussion of the nature and classification of poisonous plants there are detailed descriptions of species arranged according to families. Each plant is described according to botanical characteristics, distribution and habitat, poisonous principle, conditions of poisoning, symptoms, and treatment. The principal species are illustrated by full page drawings, showing general appearance together with details of flowers, fruit, seed, and roots. There are numerous citations of literature from a long list of books and periodicals. A good index facilitates reference.

Sinnott, E. W. and L. C. Dunn. 1939. Principles of Genetics. Third Edition. xiv + 408 p. 145 fig. *McGraw-Hill Company. New York.* \$3.50. The rapid progress in the development of genetics has called for a third edition of this well-known text. The new material relates chiefly to improved cytological methods, the application of radiation to the study of mutation, the analysis of genetic effects on development, and the use of statistical methods in the study of populations. These have resulted in the development of physiological and evolutionary genetics. New material has been added also in the field of cytoplasmic inheritance and in that of multiple factor inheritance. This has made necessary the rewriting of much of the book in order that its length be not greatly increased. These and other changes bring the text up to date and guarantee its continued usefulness.

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PROCEEDINGS

BUSINESS MEETINGS OF THE ECOLOGICAL SOCIETY OF AMERICA AT RICHMOND, VIRGINIA, DECEMBER 27 AND 29, 1938

Meeting of December 27, 1938

The Society met at Cabannis Hall at 8:50 A.M., President H. C. Hanson, presiding, and twenty-six members present.

The president appointed a Nominating Committee consisting of: R. E. Coker, *Chairman*, W. P. Taylor and W. S. Cooper; a Resolutions Committee consisting of: C. C. Adams, *Chairman*, W. T. Penfound and Raymond Pool. He also named H. de Forest, *Chairman*, of the Western Section of the Ecological Society of America for 1939. Z. P. Metcalf made an announcement concerning the field trip to the Dismal Swamp.

There being no further business to transact, the meeting adjourned at 9:06 A.M.

Meeting of December 29, 1938

The Society met at Cabannis Hall at 2:14 P.M., President H. C. Hanson, presiding, and thirty-seven members present. After the Minutes of the preceding business meeting had been read and on motion duly seconded, approved, reports of officers and committees were called for.

REPORT OF THE TREASURER

December 8, 1937 to November 30, 1938

RECEIPTS

Balance from former treasurer, Orlando Park	\$	507.56	
Royalty, <i>Naturalists' Guide</i>	\$	8.35	
Contributions for <i>Biological Abstracts</i>		10.00	
Contributing memberships		22.00	
Dues from members		2,193.16	2,233.51
			<hr/>
			\$2,741.07

DISBURSEMENTS

Royalty, <i>Naturalists' Guide</i> (V. E. Shelford)	\$	8.35
H. de Forest, Committee, Denver Meeting, 1937		23.07
V. E. Shelford, Committee		40.00
ECOLOGY, payments for members		1,224.00
ECOLOGICAL MONOGRAPHS, payment for members		363.00
Treasurer's office: supplies, postage, and clerical help		95.64
Secretary's office: supplies, postage, clerical help and travel		172.23

Printing, <i>Bulletin</i> , letterheads, etc.	249.24	
Bank charges80	2,176.33
Balance, November 30, 1938	\$ 564.74	
		<u>\$2,741.07</u>

Respectfully submitted,

STANLEY A. CAIN, *Treasurer*

I have examined the records of Stanley A. Cain, Treasurer of the Ecological Society of America, for the period December 8, 1937, through November 30, 1938, and certify the foregoing statement of receipts and disbursements is in agreement with the records. The bank balance was verified with the bank. All disbursements were made by check and supported by properly approved vouchers with the exception of checks to Ecology and Ecological Monographs. Receipts of dues from members were not traced to members' accounts.

W. H. READ, *Auditor*

The report of the Treasurer, on motion, duly seconded, was accepted.

REPORT OF THE SECRETARY

Total membership as of December 31, 1937.....	751	
Losses as of December 15, 1938:		
Deceased	7	
Cancellations	30	37
Associate	3	
Active	26	
Sustaining	1	714
		<hr/>
Additions as of December 15, 1938:		
Associate	5	
Active	46	
Institutional	1	
Sustaining	4	56 770
		<hr/>
Members removed from mailing list for arrears	39	731
		<hr/>
Total membership as of December 20, 1938	731	

Respectfully submitted,

ORLANDO PARK, *Secretary*

The report of the Secretary, on motion, duly seconded, was accepted.

At the invitation of the President, the Secretary stated that during his three-year term of office, in addition to the financial support of the Society. Northwestern University had supplied him with secretarial service for forty hours a month at \$20.00 a month and an average of an additional \$5.00 a month for postage and supplies, adding to a total contribution of \$300.00 a year for three years.

The Secretary further stated that he had been unable to print the Constitution of the Society as recommended by the Executive Committee meeting at Indianapolis last December due to a number of inconsistencies which had entered the Constitution as a consequence of the several amendments and by-laws passed by the Society at its business meetings within recent years. It was moved and seconded that the President appoint a Constitutional Committee to harmonize the present Constitution and that the Committee be further authorized to propose any additional amendments or modifications to the Constitution which are considered necessary. The motion was carried.

The President appointed a Constitutional Committee as follows: Orlando Park, *Chairman*, George D. Fuller, Chancey Juday, and A. O. Weese.

It was moved by Paul B. Sears that the Treasurer be authorized to establish a reserve, or sinking fund, to which \$100.00 or more be transferred each year as conditions of the Treasury warrant. Disbursements from the reserve fund only to be made on recommendation of the Executive Committee. The motion was seconded and carried.

REPORT OF THE BUSINESS MANAGER OF ECOLOGY FOR THE FISCAL YEAR, DECEMBER 1, 1937–NOVEMBER 30, 1938

RECEIPTS

Cash on hand (Statement of 1937)	\$ 215.44	
Dr. Stanley A. Cain, Treasurer, E. S. A.		
39 memberships 1937 at \$3.00	\$ 117.00	
435 memberships 1938 at 3.00	1,305.00	
17 memberships 1939 at 3.00	51.00	
1 membership 1940 at 3.00	3.00	1,476.00
Subscriptions: 1938	\$1,643.91	
1939	536.35	
1940	8.50	\$2,188.76
Advertising		80.00
Single numbers and back volumes		171.44
Authors' excess illustrations		
George B. Rigg		50.00
Authors' excess pages		
Dr. Willis A. Eggler		21.90
Subsidy from Brooklyn Botanic Garden		300.00
		<u>\$4,503.54</u>

DISBURSEMENTS

Printing

Lancaster Press, Inc.

	Issue	Reprints	
October, 1937	\$	\$ 25.98	
January, 1938	1,010.97	41.93	
April	1,056.75	48.08	
July	863.29	39.39	
	<u>\$2,931.01</u>	<u>\$ 155.38</u>	\$3,086.39

Illustrating

Ad Plate Engraving Co.

January, 1938	\$ 58.68	
April	69.82	
July	139.58	
October	43.85	311.93

Advertising 115.32

Purchase of Back Volumes 30.14

Office Expenses

Business:

Accounting service 12 months at \$10.00	\$ 120.00
Postage	80.25
Expressage	15.80
Stationery	12.50
Wrapping paper and twine	21.41

Editorial

Dr. George D. Fuller	35.30	
Dr. Alfred Emerson	15.00	
Dr. Robert Gregg	32.00	332.26

Miscellaneous

Audit of books for last fiscal year	\$ 5.00	
Refunds on subscriptions	6.60	
Printer's set-up composition	2.00	
Collection charges80	14.40

Balance, November 30, 1938 \$ 613.10 \$4,503.54

Cash in bank \$ 313.10

Check on hand (Subsidy) 300.00

\$ 613.10

Examined and found correct December 20, 1938.

H. P. SHOENBERNER, *Auditor*

STATEMENT SHOWING ASSETS AND LIABILITIES

DECEMBER 1, 1937–NOVEMBER 30, 1938

Assets

Cash in bank	\$313.10	
Check on hand	300.00	\$613.10

Bills Receivable

Subscriptions: 1937	\$ 8.20	
1938	13.00	
1939	37.00	58.20

Back volumes	18.00	
Advertising	92.00	\$781.30

*Liabilities**Bills Payable*

Lancaster Press, Inc.

Printing of October issue \$655.37

Assets over liabilities \$125.93

Circulation data as per mailing-list for the October issue:

	1937	1938
1. Members of the Ecological Society	520	521
2. Subscribers	411	440
3. Exchanges	87	84
4. Advertisers	21	22
5. Editorial Office	2	2
	<u>1,041</u>	<u>1,069</u>

Number of copies ordered printed per issue 1,500

C. STUART GAGER, *Business Manager*

It was moved by Dr. George D. Fuller that the report of the Business Manager of *ECOLOGY* be accepted, subject to auditing. The motion was seconded and carried. The auditor's report was subsequently received.

At the request of the Executive Committee, it was moved by A. O. Weese that a committee be appointed by the President to make a study of the business transactions concerned in the publication of *ECOLOGY*, and that this committee should have a report prepared for the Society at its next annual business meeting. The motion was seconded and carried. The President then appointed this committee as follows: R. E. Coker, *Chairman*, Alfred Emerson, and Stanley A. Cain.

REPORT OF THE EDITORS OF ECOLOGICAL MONOGRAPHS

During 1938, 655 pages were published as compared with the 547 pages for 1937. The Editors take this opportunity to thank the members of the Editorial Board for their excellent cooperation during the year.

On behalf of Dr. R. O. Rivera, Business Manager of *ECOLOGICAL MONOGRAPHS*, we present the following report for *ECOLOGICAL MONOGRAPHS* for the fiscal year ending June 30, 1938:

INCOME		EXPENSE	
Advertising	\$ 340.00	Advertising	\$ 236.00
Subscriptions	1,717.75	General expense	9.00
		Postage	13.00
		Printing	3,682.25
	<u>\$2,057.75</u>		<u>\$3,940.25</u>
Deficit	\$1,882.50		

The circulation of this journal is as follows:

Paid subscriptions	210
Duke University Library exchanges	19
Free exchange and complimentary	27
	<hr/>
	256

A. S. PEARSE,
C. F. KORSTIAN,
Joint Editors

Dr. George D. Fuller expressed the feeling of the Society in appreciation of the attitude of the Duke University Press in regard to the publication of ECOLOGICAL MONOGRAPHS. The report of the Editors of ECOLOGICAL MONOGRAPHS on motion was duly seconded, and accepted.

REPORT OF THE EDITORS OF ECOLOGY

The Editors of ECOLOGY are receiving an ever increasing supply of articles suitable for their journal with no appreciable increase in the funds available for publication. The publication of 607 pages during the year 1938, some 40 pages more than in 1937, completely exhausted the funds in our budgets; indeed, but for some unexpected payments, coming late in the year, we would have incurred a deficit. The Editors have in their files sufficient material for a volume of 550 pages in 1939; consequently, in order to meet the increasing demands for space they should be able to publish at least 700 pages during the coming year.

The Editors regret that they have not been able to meet more completely the requirements of our members. Several articles that would have done credit to our journal have been withdrawn by their authors who have sought and have obtained earlier publication elsewhere. The articles appearing in the January, 1939, issue were submitted to the editors nine to thirteen months before their publication.

The Society is thus faced with the alternative of a volume of smaller size and delayed publication of articles or a larger allowance for the journal that will permit the Editors to increase the size of the yearly issues.

Suggestions have been received recently from our publishers, the Lancaster Press, which may result in more economic publication. These suggestions include a new format for the journal which would result in a saving of approximately \$80.00 per issue. This could be done without altering the size or legibility of the page. The suggestions are being carefully studied with the possibility of taking advantage of them in 1940.

The Editors wish to express their appreciation of the cooperation and assistance so fully and cheerfully given by the members of the Editorial Board.

Respectfully submitted,

A. E. EMERSON,
G. D. FULLER,
Editors

The report of the Editors of *ECOLOGY* on motion was duly seconded, and accepted.

REPORT OF THE COMMITTEE ON REPOSITORY FOR HISTORICAL RECORDS
OF THE ECOLOGICAL SOCIETY OF AMERICA

Since there is no central repository for official records of the Ecological Society of America, and because the officers of the Society change periodically, there is a great risk of losing records that may prove of considerable interest and value in the future.

The value of ecological work has *increased* greatly in recent years, and public recognition by leading thinkers and public officials has come as a result of the solid advance made in the science. The history of any important scientific advance should be properly documented, and this cannot be done without the hearty support of the members of our Society.

The Committee of your Society on the preservation of such records, has not found much interest in this subject. They are seeking a central repository where such documents can be accumulated and properly cared for. The substantial assistance of all members is solicited by the members of your committee. As Chairman of the Committee, I would be pleased to hear from all *former* officers of the Society regarding the amount and condition of the official files in their possession, so that we may be able to plan to better advantage.

We recommend that the committee be continued.

Respectfully submitted,

C. C. ADAMS, *Chairman*

The report on motion, duly seconded, was accepted.

REPORT OF THE COMMITTEE ON SUMMER SYMPOSIA

Your committee reports that a symposium on *Influence of Fire on Wildlife and Public Welfare* was arranged and given at the Ottawa meeting 9:00 A.M., June 30, 1938, under the chairmanship of Dr. C. C. Adams, New York State Museum, Albany, N. Y. The following papers were presented:

Fire in Modern Forest Management. I. T. Haig, U. S. Forest Service, Washington, D. C.

Fire and Wildlife. Hoyes Lloyd, National Parks Bureau, Ottawa, Canada.

Fire and Land Use. H. C. Hanson, North Dakota Agricultural Experiment Station, Fargo, North Dakota.

These arrangements involved a considerable amount of correspondence, because of the international character of the program, limitations of time, and the number of organizations concerned.

Plans are now under way for future symposia, and at the request of officers of the society, these include not only the joint A. A. A. S.—Ecological-

Society Symposia for summer meetings, but some suggestions for the winter meetings as well.

The committee has in mind the increasing responsibility of ecology in matters of public policy and the need for consideration of broad problems which involve the social as well as the natural sciences.

The schedule of future meetings to which our attention will be given is as follows: Milwaukee, summer, 1939; Columbus, December, 1939; Seattle, summer, 1940; Philadelphia, December, 1940. Your Committee now consists of: Paul B. Sears, *Chairman*, 3 years, J. M. Aikman, 3 years, George E. Nichols, 2 years, A. H. Wright, 2 years, R. E. Coker, 1 year, C. F. Korstian, 1 year.

Respectfully submitted,

PAUL B. SEARS, *Chairman*

The report on motion, duly seconded, was accepted.

REPORT OF THE COMMITTEE ON THE PRESERVATION OF NATURAL CONDITIONS

The Chairman, Dr. A. O. Weese, presented a brief oral report of the activities of the committee during the year. His committee then presented the following resolution:

WHEREAS: the Great Plains of North America constitute one of the nation's greatest economic problems on account of droughts, grasshoppers, erosion, etc., and

WHEREAS: there are no large natural reserves of grassland such as exist in the case of forests;

BE IT RESOLVED: that the Ecological Society of America approves and endorses the action of the Committee on the Preservation of Natural Conditions in its unanimous vote to support the National Park Service in its efforts to set aside a Great Plains National Monument, which will serve as a check area, which may be managed on a hands-off basis and defended because of its historical value while being available for scientific research.

Respectfully submitted,

A. O. WEESE, *Chairman*

The report, including the resolution, on motion, duly seconded, was accepted, and the resolution adopted.

Dr. Weese stated that, since office facilities had been supplied by the University of Oklahoma; and there had been no occasion for extensive campaigns, the funds provided in the budget had not been expended. Dr. Weese asked that a like sum (\$50.00) be set aside for the year 1939, in addition to the credit of \$22.00 accruing to the Committee during 1938 on account of Contributing memberships.

It was moved and seconded that the sum of \$72.00 be allocated for the expenses of the Committee on Preservation of Natural Conditions for the following year. The motion was carried.

It was moved and seconded that the Committee be continued. The motion was carried.

REPORT OF THE COMMITTEE FOR THE STUDY OF PLANT AND ANIMAL COMMUNITIES

After having organized and been chairman of this committee since 1931, Dr. V. E. Shelford resigned May 1, 1938, and the present incumbent was appointed by the President of the Ecological Society to serve out the year. The committee under the Chairmanship of Dr. Shelford and with Dr. R. E. Yeatter, Secretary, has been active in recent months in the preparation of two reports for publication.

One of these concerns land holdings of North American universities. These lands are classified as to distance from the university, location in various ecological biomes, and are described briefly as to size, ecological character, and whether the vegetation is natural or second growth. Special stress was placed on completing the list for the grassland area.

The other report is a list of existing and needed reserves of natural conditions in North America from, and including, Mexico northward. Eighty-eight areas, aside from proposed national parks in Mexico, are included as being especially important, and comments concerning their size, biological character, and need for buffering are available in most instances. A map showing their location was also made.

The present Chairman has made an effort to extend this list of reservations to include Central America and the West Indies. The report on these areas is not complete as a dozen or more areas are being investigated further. Much of this region, especially in Central America, is now nearly virgin jungle and penetrable with difficulty so that active efforts for preservation of representative samples seems unnecessary, although some efforts of this kind might be expended in the West Indies.

It is hoped that the listing and preliminary investigation of these areas will serve useful purposes. Ample samples of all ecological communities should be preserved for the future, and this should be insured before suitable areas become badly disturbed. These sample areas should be representative both of plants and animals and in as nearly virgin condition as possible. The establishment of buffer areas around such reservations needs consideration in all cases, including those already set aside. The listing of these areas should call attention of ecologists to their availability for study in detail so that monographs on the various communities may eventually be worked out. Such studies would be valuable not only from the theoretical point-of-view, but also to serve as a basis for manipulating nearby areas of similar type in

a wild-life program. The location of generally smaller areas near to and owned by universities should aid in such studies. In certain instances the establishment of a definite research center might need to be urged by this society in areas where universities or other research facilities are not available.

The following financial statement is the report of Drs. Shelford and Yeatter covering the expense of the questionnaire and preparation of the summary of replies on land holdings of universities:

Letterheads	\$ 7.00
Envelopes	1.00
Mimeographing questionnaire	9.85
Postage	6.04
Typing	1.20
Mimeographing and mailing reports to contributors	14.91
Total paid by the Ecological Society of America	\$40.00
Additional expense provided from contributions, not itemized	27.50
Grand Total	
	\$67.50

Respectfully submitted,

S. CHARLES KENDEIGH, *Chairman*

The report on motion, duly seconded, was accepted.

It was moved and seconded that \$50.00 be allocated for the expenses of the Committee for the Study of Plant and Animal Communities for the following year. The motion was carried.

It was moved and seconded that Dr. S. Charles Kendeigh continue in the Chairmanship of the Committee for the Study of Plant and Animal Communities for the following year. The motion was carried.

THE REPORT OF THE COMMITTEE ON APPLIED ECOLOGY

Applied ecology is an aspect of human ecology. It involves the whole problem of a satisfactory adjustment of man to environment. The means of such adjustment is also the means whereby man has disturbed his environment and become the dominant organism in it. This means is the whole range of activities peculiar to man and known as human culture. It follows that any measures of applied ecology must work through the existing culture in order to be effective. For this reason the ecologist must remember that much of the difficulty which he is now called upon to correct was caused by measures which once had the full approval of society. This is true of exploitation of forests and soil, use of streams for industrial wastes and elimination of wild life. Nothing is to be gained by condemnation of the past. The proper strategy is to make clear to the general public that such measures are no longer socially desirable.

The most acute practical problem is to encourage the cooperation of all agencies interested in the many phases of conservation. A splendid lead has been taken by the American Wild Life Federation which is eager to have the best ecological counsel. Through this organization and its state branches, members of the society can exert a powerful influence.

It may be taken as an axiom that where two different conservation agencies find themselves in conflict, one or both is seeking a partial or immediate instead of a permanent solution. Ecologists can be of great service in the adjustment of such difference.

Essentially, the problem of adjustment of man and environment requires a sense of perspective in time and space which only the ecologist can supply. The landscape of a continent like North America is closely integrated. The condition of one part affects the rest and the events of today affect tomorrow. Here again, ecologists can be of service by guiding away from solutions that are merely partial, expedient or temporary.

It is encouraging to know that many elements in our business life are accustomed to thinking in actuarial terms, of results over wide areas and over long periods of time. Such agencies will lend a ready ear to sound ecological advice.

Finally, many recommendations of the ecologists must be supported by much better programs of land-use than are now available. Ecologists can do much to make clear that this is a scientific matter of the first importance and not a political issue.

In connection with land use planning, the Committee on Applied Ecology is offering assistance in several states to Boards of Conservation. With continued activity of the committee and with the aid of members of the Ecological Society, more contacts can be made with Boards of Conservation, and more assistance can be given.

The committee is attempting to keep informed on recent developments in land-use planning research, and will serve as a clearing house for the presentation of problems of this nature by members of the Society and others.

Although all of the problems coming to the attention of this Committee can be directly or indirectly classified as land-use problems, definite progress has been made at several points in our attack on the entire program of the committee.

1. Assistance has been given to the Maryland Outdoor Life Federation in the conservation of water resources.

2. A sub-committee has been appointed and is working with the Bureau of Economics and its state cooperative agencies on an ecological basis for the forecasting of crop yields. This committee is made up of the following men actively engaged in experimental work on the three crops now under investigation: corn, wheat and cotton: E. A. Helgeson, North Dakota State College; J. Arnold King, Bureau of Agricultural Economics; Dr. H. H.

Laud, Kansas State College; Dr. J. D. Sayre, Ohio Agricultural Experiment Station; and Dr. J. M. Aikman, Iowa State College.

3. A sub-committee is being organized to work in an advisory capacity with the Division of Research of the Soil Conservation Service.

4. The committee is making a study of the ecological problems involved in the work of the Biological Survey, especially as it relates to the research program of the Survey. In connection with the work program of the Survey, the committee is acting in an advisory capacity through the different regional offices, especially with the New England Region.

5. The committee has been asked by A. F. Dachnowski-Stokes of the Bureau of Plant Industry, to study his report on the "Problems concerning the Nation's peat and muck resources and their uses," and to recommend some action to the Ecological Society.

The committee wishes to compliment Dr. Dachnowski-Stokes on his comprehensive presentation of the problem and its solution, and to recommend to the Society the following resolutions or others of like purport:

1. The Ecological Society of America begs to recommend to the Director of the Bureau of the Census that proper action be taken to effect an inventory of acreage of peat and muck and to tabulate and publish the data in such manner as to indicate (a) unreclaimed, (b) cultivated, (c) industrially utilized, and (d) abandoned (burned-over, etc.) areas of peat and muck.

2. The Ecological Society of America recommends to the Secretary of Agriculture the standardization, through the Bureau of Plant Industry, of the commercial grades of imported and domestic peat and muck, and the setting-up of specifications to protect the consumer and to subserve the public interest.

Respectfully submitted,

H. C. HANSON, *Chairman*

(Report presented by J. M. AIKMAN)

It was moved and seconded that the Committee on Applied Ecology be continued and that the report of the Committee including the two resolutions be accepted. The motion was carried.

REPORT OF THE REPRESENTATIVE OF THE SOCIETY ON THE COUNCIL OF THE UNION OF AMERICAN BIOLOGICAL SOCIETIES

The following items were discussed at the meeting of the Council:

1. E. D. Merrill reported that there were no new developments during the year concerning an International Union of Biological Societies.

2. J. F. Flynn, reporting for BIOLOGICAL ABSTRACTS, stated that the threatened suspension of this journal had been averted and that the journal was on the road to permanent success. He stated that the minimum budget for 1938 was \$40,000 for 15,000 abstracts; 10 issues holding 17,000 abstracts have been published in 1938. By September 700 journals were represented and 850 in November. The prompt publication of abstracts and indexes was

being hastened. The sectional publication method appears to provide opportunity for control by national societies of abstracting and publishing in their field.

Colonel Hitchens, reporting for BIOLOGICAL ABSTRACTS, reported that the Microbiology Section could be maintained on 1,000 subscriptions, and that the bacteriologists would be asked for \$500.00 this year for the support of this Section. A committee of bacteriologists will manage this Section with the help of J. F. Flynn.

The necessary society support has been outlined already in a statement sent to the presidents of various organizations.

3. Oscar Riddle, reporting for the Committee on Biological Science Teaching, stated that \$10,000 had been granted by the Carnegie Corporation for expenses of the Committee of National Association of Biology Teachers-Secondary Schools' "American Biology Teacher" (new journal). It was also reported that there are now some 2,300 members. Suitable material for their journal was solicited from professional biologists. Support of professional biologists for local units of this Society was indicated as desirable in order to increase the appreciation of science. High school biology teachers are appreciating the helping hand of professional biologists, and this Society with its journal affords an outlet for the professional biologist.

4. New societies applying for membership in the Union of American Biological Societies: National Association of Biology Teachers.

Respectfully submitted,

H. C. HANSON, *Representative*

Dr. Hanson's report was generally discussed. It was moved by H. L. Shirley that this meeting go on record as urging the Trustees of BIOLOGICAL ABSTRACTS to publish "Plant Ecology" under Section D, "Animal Ecology" under Section B, and both divisions under Section A.

The motion was seconded and carried.

It was moved by J. M. Aikman that the problem of the support of BIOLOGICAL ABSTRACTS by the Ecological Society of America and any additional recommendations on resectioning of BIOLOGICAL ABSTRACTS be submitted to the Executive Committee of the Society with power to act.

The motion was seconded and carried.

REPORT OF THE COMMITTEE ON THE SALE OF THE NATURALISTS' GUIDE

When your committee began work in May, 1937, Williams and Wilkins Co., the publishers of the NATURALISTS' GUIDE, had had on hand 464 copies bound and 2109 copies in sheet form—a total of 2573 copies. As reported at the Indianapolis meeting, the publishers agreed to allow members of the Ecological Society of America to order an unlimited number of copies of the GUIDE at \$2.50 each with postage prepaid. This still gave a small return to the Society.

As a result of considerable effort, 109 copies were sold during the first six months of 1938 as against 24 copies in 1937 and 17 copies sold in 1936. The publishers profess to be encouraged despite the small number actually sold. From this experience I submit the following recommendations and comments:

1. The available stock of copies of the NATURALISTS' GUIDE will last for years.

2. Its sale at present depends primarily on its recommendation to students by their instructors.

3. The suggestion originally made by Professor V. E. Shelford should be adopted. This recommendation is that Mr. Percy Viosca or some one member of the General Biological supply house or both be appointed distributors of the occasional publications of the Society on a commission basis.

4. That continued publicity be given to the availability of the NATURALISTS' GUIDE at \$2.50 postpaid in the BULLETIN and in ECOLOGY.

5. That my resignation as Chairman of this committee be accepted.

Respectfully submitted,

W. C. ALLEE, *Chairman*

It was moved and seconded that the committee be discontinued and the report be accepted. The motion was carried.

REPORT OF THE REPRESENTATIVE OF THE SOCIETY ON THE NATIONAL RESEARCH COUNCIL

In the absence of the Representative, Dr. T. H. Frison, no report was given.

REPORT OF THE RESOLUTIONS COMMITTEE

I

WHEREAS: the Ecological Society of America has long been on record in support of the Quetico-Superior program for an international wilderness sanctuary among the border lakes of Ontario and Minnesota, and

WHEREAS: the program seeks to take a great geographical unit lying in two friendly countries and to treat it, so far as possible, as a unit under ecological principles for the perpetuation of its native plants and animals, and

WHEREAS: this forested lakeland, with its age-old scheme of plant and animal life, those of both land and water, offers an outstanding opportunity both for the study and practice of ecology,

THEREFORE: BE IT RESOLVED: that the Ecological Society of America reaffirms its hearty approval of the Quetico-Superior project and pledges its full support to all measures required for achievement of the project, and

BE IT FURTHER RESOLVED: that the Society particularly petitions Congress for a special appropriation sufficient to permit immediate purchase by

the federal government of available private lands in the Minnesota portion of the proposed Quetico-Superior area.

II

WHEREAS: Dr. Orlando Park is retiring from the Secretaryship of the Ecological Society of America, and

WHEREAS: he has served the Society with zeal and distinction, and has contributed most generously of his time, energy and ability,

BE IT THEREFORE RESOLVED: that the Ecological Society of America, at its annual meeting at Richmond, Virginia, express its deepest appreciation for his services as Secretary.

III

WHEREAS: the Ecological Society of America has greatly enjoyed and profited from the fine arrangements that the Local Committee for the Richmond meeting of the A. A. A. S. have provided for its annual meeting, and

WHEREAS: the Society sincerely appreciates the lavish hospitality and courteous consideration with which our visit to Richmond and Virginia has been marked,

BE IT RESOLVED: that the Ecological Society of America express in this formal, yet most sincere way, its appreciation of all these many favors in general and to its individual members in particular, and

BE IT FURTHER RESOLVED: that this expression be incorporated in the Records of the Society, and that a copy of these Resolutions be forwarded to the Chairman of the Local Committee for the Richmond meetings of the American Association for the Advancement of Science.

Respectfully submitted,

C. C. ADAMS, *Chairman*

W. T. PENFOUND

RAYMOND POOL

The report on motion was duly seconded and unanimously accepted.

REPORT OF THE COMMITTEE ON NOMENCLATURE

A set of definitions "and terms suggested for defining" has been assembled by the committee and is submitted with the recommendation that the list be widely circulated among the Society membership during the coming year so that the definitions can receive careful study. No definition deserves formal approval by the Society until it has been given mature thought and is well written. Much improvement appears necessary before publication by the Society is warranted. In accordance with the originally authorized duties (see *ECOLOGY* 12: 437-8, 1931), the chief purpose in submitting this list is to aid in the clarification of ecological terminology and to encourage more

precise usage of terms. Occasionally, it has seemed appropriate that the committee should recommend to the Society that certain terms be designated as desirable or undesirable, not with the idea of being dogmatic or arbitrary, but to aid in the development of ecological terminology based upon critical consideration by many ecologists over a period of several years. It is not intended that this list should be a complete glossary. Many terms have been purposely omitted for various reasons. For instance: certain words have had such limited usage that their consideration by the committee did not seem justified.

A special Soil Science Subcommittee, consisting of Joseph Kittredge, Jr., *Chairman*, S. O. Heiberg, H. J. Lutz, and J. T. Auten, contributed most of the definitions pertaining to soils. The Committee wishes to express appreciation to this subcommittee as well as to numerous individuals who have contributed suggestions.

Although it has not been possible to adhere closely to any set rules, some of the basic principles of nomenclature which have guided the work of the committee may be stated as follows:

1. Natural growth of ecological terminology should not be hampered by rules. The committee has attempted, however, to serve as a clearing house and to point out, especially to beginners in the field, what is considered good usage. Precedent, usage, and approval of authoritative bodies are important in the selection of terms.

2. Restricted scientific usage should not violate common literary or general scientific usage.

3. Words long used in a broad sense should not be given a new and arbitrarily restricted, special meaning.

4. Uniformity of usage is desirable in the same field or in closely related fields, as forestry, agronomy, ecology, physiology, soil science, meteorology and geography. If a relatively new word is commonly accepted in one branch of science it should be adopted in other branches when it is needed there.

5. New words should be coined only when there is a distinct need. It is desirable that ecological literature be intelligible to as wide a field of readers as possible. It is not necessary to have a separate term for every slight difference of meaning.

6. Words are tools of thought. An exact term may aid in establishing a clear-cut, distinct concept. On the other hand, the too early coining of new terms or definitions may actually foster ambiguity and inaccuracy. Much care must be given to the choice of appropriate terms so that the writer or speaker can convey to others his exact shade of meaning. The committee believes that the definitions given in the list will help to make ecological terms more efficient tools of thought.

The committee needs criticism, rewritten definitions, and new definitions for terms not defined, from all possible sources so that a list of some generally approved definitions may be submitted to the 1939 annual business meeting of the Society with the recommendation to publish. The committee will also appreciate receiving approval or disapproval of the present list and definitions. It is a pleasure to report that an increasing number of scientists in fields closely related to ecology are aiding the work of this committee. Several organizations such as the Soil Science Society of America and the Society of American Foresters have extended cooperation in securing clarification and increasing uniformity in usage.

Requests for a copy of this report should be accompanied by 6 cents in postage.

Respectfully submitted,

HERBERT C. HANSON, *Chairman*

FRANK E. EGGLETON

C. F. KORSTIAN

Z. P. METCALF

L. E. NOLAND

It was moved and seconded that the report be accepted and the committee continued. The motion was carried.

REPORT OF THE COMMITTEE ON NOMINATIONS

Your committee submits the following nominations:

President: Charles T. Vorhies.

Vice-President: C. F. Korstian.

Secretary: W. J. Hamilton, Jr., for three years.

Editorial Board of Ecology: H. I. Baldwin, H. J. Oosting, T. I. Storer,
L. R. Dice.

Editorial Board of Ecological Monographs: P. L. Errington, E. T. Wherry.

Representative to Union of American Biological Societies: Orlando Park,
H. J. Lutz.

For Committee Member on Executive Committee: A. O. Weese.

Respectfully submitted,

R. E. COKER, *Chairman*

W. P. TAYLOR

W. S. COOPER

It was moved by Alfred Emerson that the Secretary cast a unanimous ballot for the report of the Nominating Committee. The motion was seconded and carried. The officers named in this report were declared elected.

In view of the unavoidable absence of the newly elected officers, Dr. H. C. Hanson continued in the Chair and called for new business.

It was moved by Stanley A. Cain that the President be authorized to write a letter expressing the friendly greetings of the Society to Dr. Henry C. Cowles of Chicago. The motion was duly seconded and carried.

It was moved and duly seconded that the meeting stand adjourned. The motion was carried.

Adjournment at 5:09 P.M.

ORLANDO PARK, *Secretary*

NOTES AND COMMENT

PLANT SUCCESSION ON SCORIA BUTTES OF WESTERN NORTH DAKOTA

One of the most interesting phytogeographic regions in the country is the so called "Badlands" area of Western North Dakota.

On the "scoria"¹ buttes of these badlands there has been initiated a rather unique type of plant succession.

Kellog² has reported that the soil is highly alkaline and hence only those plants that are alkaline tolerant can gain an early foothold and ecize. In addition to this, the plants must also be able to anchor themselves in order to survive the active erosion which accompanies the heavy torrential rains characteristic of this region. Because of these conditions most of the pioneer species are perennials with tap roots, especially on the steep slopes.

Those species most common are *Artemisia longifolia* Nutt., *Artemisia dracunculoides* Pursh, *Atriplex argentea* Nutt., *Atriplex hastata* L., *Chrysothamnus* sp., *Eriogonum multiceps* Nees, and *Salicornia herbacea* L.

Second weed stage. On the more gentle sloping sides of the buttes and paralleling the steeper areas where the erosion has been somewhat checked, a more representative group of plants tend to invade. The kinds of species invading these areas vary, depending upon such factors as soil structure, amount and kind of salts in the soil, drainage conditions, moisture and temperature conditions prevailing during germination and growth; and kind and proximity of parent plants to supply the disseminules. There is an increase in the number of plants of the pioneer weed stage and in addition other species tend to make their appearance as soil conditions are improved and erosion is decreased. The most common invaders are *Chenopodium leptophyllum* Nutt., *Polygonum erectum* L., *Polygonum aviculare* L., *Lepidium densiflorum* Schrad., *Grindelia squarrosa* (Pursh) Dunal, and *Salsola pestifer* A. Nels. In some instances *Agropyron Smithii* Rydb., and *Distichlis stricta* (Torr.) Rydb., appear during the latter part of this stage.

In areas receiving drainage from higher lying ground, an accumulation of salt may occur and the vegetation be kept in a subclimax stage consisting of the *Atriplexes*, *Artemisias*, *Salicornia*, *Distichlis*, and *Agropyron Smithii*.

First grass stage. In the first grass stage the soil affords slightly better growing conditions than in the late weed stage. The penetration of water has been increased with a resultant leaching of salts. The death and decay of numerous small roots each year improves the physical and chemical conditions in the surface soil at least. An increase of *Agropyron smithii* occurs and in addition other perennial grasses such as *Andropogon scoparius* Michx., *Carex* sp., *Agropyron spicatum* (Pursh) Scribn. and Smith, *Poa* sp., *Calamovilfa longifolia* (Hook.) Hack., *Bromus inermis* Leyss., *Koeleria cristata* (L.) Pers., *Stipa viridula* Trin., *Bouteloua gracilis* (H. B. K.) Lag., and *Bouteloua curtipendula* (Michx.) Torr., make their appearance. Many of the forbs found in the second weed stage persist but their abundance has decreased.

Climax. With the continual improvement of the soil conditions accompanying the vegetational development, the grasses reach their greatest significance. Gradually the *Agropyrons*, *Carex*, *Stipa viridula* and the *Boutelouas* assume more importance and be-

¹ Term applied to baked shale and limestone produced by burning lignite beds.

² Kellog, Chas. E. 1934. Morphology and genesis of the solonetz soils of western North Dakota. *Soil Sci.* 38: 483-501.

come the dominant grass species. *Calamovilfa longifolia* is a consociation on the lighter or sandy soils in this area.

Intermingled with the perennial grasses are such forbs, shrubs and trees as *Malvastrum coccineum* (Pursh) Gray, *Lygodesmia juncea* (Pursh) D. Don., *Hedcoma hispida* Pursh the Artemisias, *Dasiphora fruticosa* (L.) Rydb., *Rhus trilobata* Nutt., *Rosa* sp., *Elaeagnus argentea* Pursh, *Shepherdia argentea* Nutt., *Juniperus virginiana* L., *Juniperus horizontalis* Moench., and *Juniperus communis* L. The last mentioned is rare and usually confined to the north slopes.

Post climax. In favored areas as along the stream beds a post-climax vegetation of trees is found. *Fraxinus lanceolata* Borck., *Quercus macrocarpa* Michx., *Acer Negundo* L., *Populus deltoides* Marsh., *Salix* sp., *Prunus virginiana* L., *Prunus americana* Marsh., *Ulmus americana* L. and *Amorpha fruticosa* L., are the dominant species.

The successional stages of vegetational development are not clear cut for the seres, as shown by Hanson and Whitman³ but are dependent on the soil development.

B. IRA JUDD.

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³ Hanson, H. C., and W. Whitman. 1937. Plant succession on solonetz soils of western North Dakota. *Ecology* 18: 516-522.

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THE SOCIAL HIERARCHY IN RING DOVES¹

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INTRODUCTION

Social organization is exhibited in flocks of birds. Investigation in this field was initiated by Schjelderup-Ebbe ('24, '31). In a summary of his studies ('35), he says, "One of the points which the recognition of each individual in the flock of the same species makes it possible to observe is that there exists among birds a definite order of precedence or social distinctions." He states that in over fifty species observed, one bird invariably has precedence over another. This precedence in rank, he asserts, is founded upon despotism. Stimulated by the work of Schjelderup-Ebbe, various studies in this field have been undertaken at the University of Chicago and elsewhere. Masure and Allee ('34a) and Murchison ('35) confirm Schjelderup-Ebbe's observations in the case of the common chicken. Masure and Allee, however, in the case of the common pigeon ('34a) and the shell parakeet ('34b), find that the social organization is based upon a peck-dominance after many conflicts rather than a peck-right established in an initial combat. A number of studies extend the investigation to other birds and to certain other vertebrate groups. Lorenz has studied the social behavior of several birds, among them the jackdaw and the European black crowned night heron ('35), and Noble, Wurm, and Schmidt ('38), that of the American black crowned night heron. Both recognize a social organization. Lorenz finds it in both artificial associations and wild flocks of jackdaws, geese, etc., but not in the colonies of European night herons. Noble, Wurm, and Schmidt find a "hierarchy of dominance" in the American herons, an outgrowth of the struggle for food among nestlings. They conclude that this dominance is completely masked by territorial requirements in older birds except in the case of pairs. Evans ('36) finds a social hierarchy among lizards (*Anolis carolinensis*), as has Uhrich ('38) in a study of mice.

¹ The author desires to express appreciation to Dr. W. C. Allee for his suggestions and assistance and to Dr. L. V. Domm for his kindness in sexing a group of ring doves.

The present investigation of the social hierarchy in flocks of ring doves was begun for comparative purposes. Do these birds show a type of organization similar to that in flocks of common pigeons? Later the study developed into an attempt at an analysis of certain factors involved in the establishment and maintenance of the hierarchy, such as Allee ('36) has suggested in this connection.

Sexually mature blond ring doves were used, each flock confined in a cage, 25" x 26" x 32". The caged birds were housed in a laboratory of the zoology building of the University of Chicago during the summers of 1935 and 1937, and in the greenhouse of the Whitman Experimental Laboratory in the winter of 1936 and 1937. Two small flocks, under observation during the winter of 1935 and 1936 were kept in a roomy, well-lighted attic of a school building. Adequate water, grit, oyster shell, etc., were supplied at all times. Feeding was done about an hour preceding observation periods. During feeding and immediately following, few contacts between the ring doves were found to occur, hence the allowance for the interval of time. All birds remained in a healthy, active state throughout the series of observation periods except that in the last groups of experiments, wing injuries occurred in two cases.

A difficulty, which the observer encounters in the use of ring doves, is in sex recognition. Whitman ('19) refers to this in numerous instances. External morphological differences are not detectable. Behavior is the chief clue but is complicated by the simulation of the opposite sex on the part of both males and females. Whitman ('19) records the case of two males which paired, one assuming the part of a female through a whole season. He also observes, "The continual isolation of two female doves is usually sufficient to induce their mating with each other. Many of the phenomena of a normal pairing will be exhibited by such unnatural pairs." In the present study observations over two periods were discarded because of the discovery that in each a bird of opposite sex had been present in a supposedly homosexual flock. In one case the appearance of an egg was the first intimation of the presence of a female in a male flock. Isolation of the individual birds and the subsequent appearance of a second egg in the cage of one, identified the female. After this occurrence, until the fall of 1937, only birds who had histories of successful matings were used in the homosexual flocks. In 1937, some additional birds were secured and newly formed groups caged for observation. Where mating histories were unknown, behavior was at first relied upon in segregating sexes. The behavior of certain birds, soon after this separation, indicated some mistaken sex identities. A bird (*G*) in a flock supposed to be composed of females, began to show marked male behavior. On the contrary in a male flock (*D*) grew increasingly submissive. From the time the birds in this case were assembled, this bird was courted by others. To settle identities, Dr. L. V. Domm sexed ten whose mating histories were not fully known. In spite of the contrary evidence from be-

havior, *D* was found to have been correctly identified as a male. On the other hand suspicions regarding *G* were well founded for this bird proved to be a male. All data for the flock containing it were discarded.

An attempt was made to use flocks of uniform size. Complications due to failures in sex recognition, availability of animals, and injuries to wings necessitated some variations. In most of the series, flocks were made up of seven or eight birds. Individuals were banded for permanent identification. Distinguishing marks of nail enamel for use during observations were placed on heads or breasts. These were relatively inconspicuous and, so far as could be determined, were not disturbing to the organization in any flock. In order to reduce any possible affect, the marks were placed on the birds 24 or more hours before observations were begun.

The presence of an observer may have affected the flock organization. However the birds, except for a few days after first securing them, seemed entirely undisturbed so long as no hand or object of any kind was extended above a cage. The observer, while recording contacts, sat quietly on a stool about two feet from the table or shelf which supported the cage. Such activities as filling water containers, cleaning cages, etc., were cared for an hour or more preceding observations. Regularity in time and order of observation periods was maintained with but slight variation. As a rule, the early afternoon hours were used.

THE SOCIAL HIERARCHY

The first series of observations, made in July and August, 1935, were conducted in order to make comparisons of the social organization found in ring doves with that in common pigeons (Masure and Allee, '34). Periods of time corresponding to those in the study of the pigeon were used in the tabulation of the data: 14, 20, 26, and 32 days in the female flock and 12, 18, and 24 days in the male flock. In tables I and II (also III and IV) actual

TABLE I. *Peck-Dominance in a flock of five female ring doves, Summer, 1935*

Doves	14 days	20 days	26 days	32 days
<i>O:WT</i>	1:7	2:7	2:7	4:8
<i>O:RR</i>	0:0	0:0	2:0	2:3
<i>O:P</i>	1:1	1:1	1:1	1:2
<i>O:RT</i>	0:0	0:1	0:1	1:1
<i>WT:RR</i>	0:9	0:11	0:12	0:13
<i>WT:RT</i>	0:2	0:3	0:3	0:7
<i>WT:P</i>	0:1	0:3	0:3	0:5
<i>RT:P</i>	0:0	0:1	0:1	0:1
<i>RT:RR</i>	0:0	0:0	0:0	0:0
<i>P:RR</i>	0:0	0:0	0:0	1:9

Order of Dominance

<i>WT</i> (3)	<i>WT</i> (3)	<i>WT</i> (3)	<i>O</i> (3½)
<i>O</i> (1½)	<i>O</i> (2½)	<i>O</i> (2½)	<i>WT</i> (3)
<i>P</i> (½)	<i>RT</i> (1)	<i>RR, RT</i> (1)	<i>RT</i> (1½)
<i>RR, RT</i> (0)	<i>P</i> (½)	<i>P</i> (½)	<i>P</i> (1)
	<i>RR</i> (0)		<i>RR</i> (0)

TABLE II. *Peck-Dominance in a flock of nine male ring doves, Summer, 1935*

Doves	12 days	18 days	24 days
RD:WW	3:10	4:12	11:17
RD:U	3:19	5:21	7:21
RD:WD	3:11	3:14	3:14
RD:C	0:4	1:6	2:12
RD:RS	0:9	1:12	2:12
RD:RW	2:6	4:6	6:8
RD:RC	2:5	2:7	2:7
RD:V	0:3	1:5	1:8
U:WW	21:37	44:48	45:55
U:V	13:16	14:20	15:20
U:RW	2:5	6:16	11:20
U:RS	8:12	8:16	9:16
U:RC	1:8	1:13	3:17
U:WD	3:7	4:10	4:11
U:C	2:5	2:9	3:10
WW:RC	9:16	11:20	14:23
WW:V	2:12	7:16	7:17
WW:RW	1:4	3:9	8:11
WW:WD	4:6	4:11	6:13
WW:C	0:7	4:10	5:11
V:RW	1:3	3:10	4:14
V:C	0:0	1:2	1:2
V:RS	3:5	4:5	6:6
V:RC	3:1	3:3	3:3
V:WD	2:2	2:2	2:2
RC:WD	6:7	6:8	6:8
RC:RS	0:7	1:9	1:10
RC:C	2:2	3:4	3:4
RW:C	0:5	1:8	2:8
RW:WD	2:2	2:3	2:3
RW:RC	0:0	0:2	0:2
RS:WW	6:9	7:13	8:15
RS:RW	0:2	0:8	0:11
RS:WD	1:2	1:2	2:2
WD:C	1:1	1:1	1:3
C:RS	2:1	2:4	3:4

Order of Dominance

RD (8)	RD (8)	RD (8)
U (7)	U (7)	U (7)
WW (5)	WW (5)	WW (5)
RS (4)	V (4)	V, RC (3½)
RC (3½)	RC (3½)	RW, RS (3)
V (2½)	RW, RS (3)	WD (2)
WD, RW (1½)	C (1½)	C (1)
C (1)	WD (1)	

observations are summarized. The individual doves are represented by letters. Relative dominance at the end of the period of observation is indicated by the arrangement of these letters at the left of the tables. The more dominant individuals are listed to the left in any given pair.

The successive columns give the number of times of observed peck-dominance at the indicated number of days from the beginning of observations. Following the records of observed contacts, the apparent rank in the social hierarchy, referred to as the order of dominance, is tabulated. The birds are ranked according to the number of other birds over which they have dominated, this number being shown in parentheses. (The same method of tabulation has been used in all later tables where the so-called order of dominance is listed.)

In the first observation period (Summer, 1935) of 24 days in a flock of nine males, in only two of the possible contact pairs, did the same bird win all the contacts. In the female flocks contacts were comparatively few. A greater proportion of cases than in the male flock occurred in which one bird was consistently submissive, five out of ten possible contact pairs. The data in the case of the females are very limited and, it may be, that they are inadequate as a basis for conclusions. No complete sex changes in rank in the flock occurred in the males, but there was one in the female flock. The general picture in both flocks is quite similar to that in the corresponding pigeon flocks. Peck-dominance rather than peck-right prevails. The changes in rank are less numerous; on the other hand a larger proportion of contact pairs in both male and female doves are even at summarizing periods than is true of the pigeons.

The observations recorded in tables I and II were made in summer. Due to time limitations a comparison of the data from the doves with premating data only of the pigeons was permitted. To afford a more satisfactory basis for comparison, a second series of observations were made the following winter (tables III and IV).

TABLE III. *Peck-dominance in a flock of five female ring doves, Winter, 1936*

Doves	Pre-mating period			Post-mating period			Grand Total
	14 days	20 days	26 days	16 days	22 days	28 days	
P:RT	16:68	17:72	19:78	6:9	9:11	11:14	30:92
P:WT	2:24	3:31	3:37	8:7	9:8	23:8	26:45
P:RR	4:22	5:22	6:25	4:8	6:13	7:13	13:38
O:P	16:60	18:69	18:73	0:0	1:0	2:1	20:74
O:RR	1:41	1:52	2:58	0:2	3:3	4:12	6:70
O:WT	2:17	2:22	3:23	8:3	9:3	9:5	12:28
RT:O	9:52	21:55	23:57	6:4	8:10	14:18	37:75
RT:RR	2:14	2:16	7:19	2:15	2:22	2:24	9:43
WT:RT	8:3	8:3	9:14	1:112	1:113	1:114	10:128
WT:RR	4:5	5:6	7:11	2:26	2:27	2:51	9:62
Order of dominance							
R, T, P, O (3)	R, T, P, O (3)	P, O (3)	WT (4)	WT (4)	WT (4)	P, O (3)	
WT (1)	WT (1)	RT, WT (2)	P, O (2)	P (3)	P (3)	RT, WT (2)	
RR (0)	RR (0)	RR (0)	RT (1)	RT (2)	RT (2)	RR (0)	
			RR (0)	RR, O (4)	O (1)	RR (0)	

TABLE IV. *Peck-dominance in a flock of five male ring doves, Winter, 1936*

Doves	Pre-mating period			Post-mating period		Grand Total
	12 days	18 days	24 days	16 days	22 days	
RS:V	20:60	33:71	37:85	19:30	29:38	66:123
RS:U	12:47	19:53	22:56	6:49	6:61	28:117
RS:RC	16:41	16:55	23:61	4:10	5:21	28:82
RS:RD	4:44	14:48	21:51	9:13	9:18	30:69
U:RD	35:68	64:83	83:91	11:59	14:77	97:168
U:RC	34:68	48:92	56:99	5:21	9:30	65:129
V:U	34:15	45:24	55:36	38:67	48:85	103:121
V:RC	14:26	18:47	22:58	1:41	2:57	24:115
RD:V	17:3	22:25	25:41	10:4	12:8	37:49
RC:RD	5:62	14:64	19:72	7:12	10:21	29:93
Order of dominance						
RS (4)	RS (4)	RS (4)	RS (4)	RS (4)	RS (4)	RS (4)
U (3)	U (3)	U (3)	U (3)	V (3)	V (3)	U, V (2)
V (2)	RD, V, RC (1)	RD, V, RC (1)	U (2)	U (2)	U (2)	RD, RC (1)
RC (1)			RC (1)	RC (1)	RC (1)	
RD (0)			RD (0)	RD (0)	RD (0)	

From January 17 to May, 1936, observations of female and male flocks of five birds each were made. Premating, mating, and postmating records with summarizing periods, corresponding to those in the pigeon flocks, were kept. The females were the same individuals as those in the summer flock; the males, five of the original nine. The pigeon flocks were larger, seven in each, but removal of the doves from the University necessitated a reduction in the number in each lot.

In the data from the 1936 flocks much the same conditions prevail in the premating flocks as in the summer flock. Few changes in rank, one in each group, this time, but fewer "ties" than in summer, are to be noted. Many more contacts were observed in the female flock than in the summer months. Again the picture is one of peck-dominance. Observations of the heterosexual flock, composed of the combined homosexual groups, during a 12-day period, showed attempts at mating on the part of all the birds. During this period *RD* ascended from the lowest to the highest rank, dropping again to the lowest in the post-mating period (table V). It may be that he was stim-

TABLE V. *Comparison of the order of dominance in a mixed flock with that in sex-segregated flocks of ring doves in pre-mating and post-mating flocks, Winter, 1936*

Pre-mating period	Mating period	Post-mating period
Males	Mixed flock	Males
24 days	12 days	22 days
<i>RS</i> (4)	<i>RD</i> (8)	<i>RS</i> (4)
<i>U</i> (3)	<i>RS</i> (7)	<i>V</i> (3)
<i>RD, V, RC</i> (1)	<i>U</i> (6)	<i>U</i> (2)
	<i>V</i> (5½)	<i>RC</i> (1)
	<i>P</i> (4½)	<i>RD</i> (0)
	<i>RC, WT</i> (4)	
Females	<i>O</i> (3½)	Females
26 days	<i>RT</i> (1)	28 days
<i>P, O</i> (3)	<i>RR</i> (½)	<i>WT</i> (4)
<i>RT, WT</i> (2)		<i>P</i> (3)
<i>RR</i> (0)		<i>RT</i> (2)
		<i>O</i> (1)
		<i>RR</i> (0)

ulated in some way by contacts with the opposite sex to more decisive activity than in that of the homosexual flock. Except for *RD*'s rise during the period of association with the females, little change occurred in the order of peck-dominance in the male group throughout the entire series. One female (*P*) was able to ascend above *RC* in rank but no other females established dominance over males. As in the female pigeons, one bird (*WT*) appears to be chiefly responsible for the shifts among the females which occur in the three periods. It may be noted that *RR* remained consistently lowest.

In the mixed flock, three pairs of birds mated. Unlike the pigeons, most of the pecking was done by males. The females off the nest were pursued by the males and fewer pecking contacts occurred between the sexes than between males. It is to be observed that *RC* and *RR*, the first pair to mate

and to possess a nesting location, had few contacts with other birds and it was *RC* who was the only male to become subordinate to a female. It appears probable that if more ample nesting space had been provided than was done, other pairs might have become more stable. In that case, the picture might have been more like that of the pigeons', one of couples, each with few contacts with other couples.

While making the observations of the first flocks during the summer of 1935, the question arose as to whether data secured at one period of the day is typical of the remainder of the hours of activity. By way of checking upon this point a second daily period of observations in the male flock, was provided just preceding and during roosting. This period was timed so that it ended just as it became too dark to distinguish markings. It was found that pecking had almost ceased when it became this dark, if not entirely so. Examination of the data (table VI) from this period shows some striking

TABLE VI. *Comparison of daytime and evening periods in a flock of nine male ring doves, Summer, 1935*

Order of peck-dominance, 24 days

Afternoon	Evening	Total
<i>RD</i> (8)	<i>V</i> (8)	<i>RD</i> (6½)
<i>U</i> (7)	<i>WW, U</i> (6)	<i>V, U</i> (6)
<i>WW</i> (5)	<i>RW</i> (5)	<i>WW</i> (5½)
<i>V, RC</i> (3½)	<i>C</i> (3)	<i>RW</i> (5)
<i>RW, RS</i> (3)	<i>RD, WD</i> (2)	<i>C, RC, WD</i> (2)
<i>WD</i> (2)	<i>RC, RS</i> (1½)	<i>RS</i> (1)
<i>C</i> (1)		

differences from that in the early afternoon. *RD, V*, and *C* occupy quite different positions. It appears that the attempt of birds, who during the day remained on the floor or lower perches, to secure positions on the higher perch, affected the relative ranks of certain of the birds. Some birds remained on this perch practically all the time, and, during the day, drove away all others who approached. As dusk descended and the stimulus to roost grew stronger, birds customarily driven off in broad daylight, seemed to become so activated as to win pecking contacts with those on the roost, and consequently, the desired roosting space. These results at least indicate a need for observations over a greater spread of the hours of activity if a complete picture of the social organization of the flock is to be obtained. They also suggest that roosting habits are a complicating factor in connection with the territorialism existing in a flock.

With reference to territorialism, it may be remarked that some degree of this characteristic condition of bird associations, described by Howard ('20), Nice ('37) and many others, was evident in all observed flocks of ring doves. Usually one or more birds in each adopted definite locations in the cage and tended to defend these against all intruders. Usually if the bird showing territorialism left its customary perch or corner, it was compelled to return

by concerted attacks of most of its cage mates. Such behavior is reported by Taylor ('32) and by Masure and Allee ('34a) for pigeons.

In all cases observed, not only those in 1935 and 1936, but in those of the later studies to be reported in this paper, 54 sets of observations of female and male flocks in all (tables VII and VIII), a linear order of ranking is found. It is true that in all but six, at one or more points in the order, two or more birds have an equivalent status. In the males, where a comparatively high percentage of contacts occurs, the linear order is clearer than it is in the female flocks. In only two cases, female flock A, March 31, 1936, and male flock A, March 29, 1936, is there found a perfectly regular series of intervals in this linear order.

TABLE VII. *Order of peck-dominance in flocks of female ring doves during 20 observation periods, 1935-1937*

Date			No. of days	No. of birds in each rank in the social order												Total no. of birds in flock
Yr.	Mo.	Da.		5.5 ²	5	4.5	4	3.5	3	2.5	2	1.5	1	0.5	0	
1935	7	11	32					1	1			1	1		1	5
1936	1	17	26						2		2				1	5
	3	31	28				1		1		1		1		1	5
1937	1	18	16					3	1		2		1			7
	2	17	8			1			1		2		1		1	7
	2	22	16		1		1				2				2	6
	2	27	8				1		3		1		2			7
	3	29	8								4		1		2	7
	3	29	8								2	1	2	1		6
	4	8	8						3		1		1		1	6
	4	9	8				1	1			2		2		1	7
	4	18	8							1	2			3		6
	4	19	8							2	2	2	1			7
	6	17	24		2			1	1	1	1				1	7
	7	13	10						1		4	2				7
	7	23	10		1				2		1		2		1	7
	8	2	5				1				4			2		7
	8	8	10		1			1	1	2	2			1	1	7
	8	18	5				1			1	1		3	1		7
	8	23	5				1		1		1		2		2	7

² Rank in social order.

In numerous cases especially with females, very few contacts occurred between pairs during observation periods; in some none, and in some, but one, or two. It was at first deemed advisable to omit counts of one or two contacts only, since they might not be representative. After continued observations, however, it seemed more unwise to ignore them than to retain them. In some cases these few contacts seemed to be of a very decisive character. This was especially noticeable in female flocks. Such data, even if limited, give a more adequate picture of the social hierarchy than could be obtained in their absence. Since the observer spent several hours daily in the proximity of the various flocks involved, either actively engaged in recording peck-

TABLE VIII. *Order of peck-dominance in flocks of male ring doves during 34 observation periods, 1935-1937*

Date			No. of days	No. of birds in each rank in the social order																	Total no. of birds in flock
Yr.	Mo.	Da.		8 ^a	7.5	7	6.5	6	5.5	5	4.5	4	3.5	3	2.5	2	1.5	1	0.5	0	
1935	7	11	24	1		1				1			2	2		1		1			9
1936	1	17	24										1	1				3			5
	3	29	22										1	1		1		1	1		5
	10	13	24			1			2			1	2					1		1	8
	11	25	8					2				1	1	2		1	1				8
	12	3	8			1			1	1	1	1		1			3				8
	12	12	8					1	2			2				2			1		8
1937	1	2	8				1		1	1		1	2			1		1			8
	1	18	16						2	2			1					1		1	7
	2	8	16						2	1			1			1		1		1	7
	2	16	8						2			1	1			1		1	1		7
	3	1	8				1						3			1	1			1	7
	3	4	8					2								1		1		1	7
	3	9	8							1		1	2	2	1			1		1	7
	3	29	8						2			1	2					1		1	7
	4	7	8							1		1			2	2				1	7
	4	7	8					1				2	1	1					2		7
	4	16	8						2			1	1			1				2	7
	4	16	8									2	1	1		2	1				7
	4	26	8				1					1	2	1		1				1	7
	4	26	8					1				1		1		3		1			7
	6	17	24						1	1		1				2		2			7
	6	17	24									1		3				2			7
	7	13	10						1			1	1	1		1	1	1			7
	7	13	10							1	1	1	1	1		1	1	1			7
	7	23	10					1				1	1	1		2		1			7
	7	23	10						1			2		1		2		1			7
	8	2	5							1	1	2			1		2				7
	8	2	5					1		1				2		1		2			7
	8	8	10						1	1		1			1	2	1				7
	8	14	8					1				2		2				1		1	7
	8	18	5						1			1		1	2			2			7
	8	21	8						1	2				2				1		1	7
	8	23	5									2	1	2			1	1			7

^a Rank in social order.

ing contacts for one or the other of the flocks, or in other phases of this work, it was usually possible to note exceptional cases of contact in any flock and so to determine whether the behavior during observational periods were typical or not.

In general, it may be said that in the series of studies of the summer and winter of 1935 and 1936 in homosexual flocks of ring doves, and in the flocks used in experimental work in 1936 and 1937, the results obtained are similar to those found for the common pigeon and support the conclusions in that case. A definite social organization is indicated and peck-dominance rather than an absolute peck-right is the rule. That is, when two birds peck back and forth, now one retreating and now the other, the one observed to retreat the fewest times is said to have peck-dominance for that pair. It is observed

by Masure and Allee ('34) that pigeons standing high in the social order have more social contacts than those low in the scale. This is in general the situation found in the flocks of doves. In three series of observations of doves (tables II, III, and IV), the three birds in each ranking highest, had higher numbers of contacts than the remaining birds. In each of these cases the two birds lowest in rank had corresponding positions in relative number of contacts. Table I does not show such a relationship but the data in this table are quite meagre and hence may be inadequate for comparison.

COLOR AND CONTOUR AS CUES IN RECOGNITION

It seems probable that certain factors influencing the social hierarchy in bird flocks may be subject to modification. Schjelderup-Ebbe ('35) believes that age, sex, season, health, relative strength, weariness, etc., are among these modifying factors. Age may be involved, yet in this investigation the oldest bird (*RD*) in the original male flock, vacillated in rank. He was high in the social order much of the time but at others he was subordinate to two or more birds of the flock. Sex, in the common usage of the term, was not a factor in these experiments since homosexual flocks were used. Moreover it does not appear that age, sex or the other factors enumerated are sufficient to account for the establishment of the social organization which develops in the flock. When differences in these conditions were eliminated as far as possible in the flocks used, the typical linear flock order still persisted (tables VII and VIII).

A clue to the part which these and other factors play may be found in a study of the means of recognition of one another among flock members. Continued maintenance of a hierarchy implies recognition and memory. Craig ('08) has shown that voice plays a role in recognition in ring doves. This has been confirmed in the present study. Certain calls influenced, not only the flock of which the bird making them was a member, but the other flocks in nearby cages, whether of the same or the opposite sex. A certain synchrony in behavior, seemingly largely dependent upon auditory stimuli, was observed in all the cages in the room. Schjelderup-Ebbe ('35), Allen ('34), Chapman ('35), Noble and Vogt ('35), Noble ('36), Tinbergen ('35) and others have made extended observations of recognition among birds, particularly the phase having to do with sex. Noble and Vogt ('35) after experiments with mounted specimens and with artificially altered plumage characters in the redwinged blackbird and other dimorphic species, conclude that visual cues alone will produce sex responses on the part of the males in the pre-breeding season before females have come into their territories. Noble ('36), states that, "Mature Flickers apparently have learned to recognize the moustache as a badge of maleness." He adds that this badge "will call forth an attack by a territory guarding male even when artificially attached to a female apparently mated with him." Such observations, and experiments with the

cues operative in recognition, seem to have shown, as Verwey ('30) points out, that stimuli, which in birds act as a means of recognition, seem to be auditory and optical.

In the ring doves in many cases no visible color, size or contour differences, either between members of the same or opposite sexes, are to be distinguished by human observers. Moreover, failure of the birds to recognize individuals of the other sex in initial encounters, seems to be evidence that visual cues of color, size, and contour are not operative among the birds themselves. It is because of this that Whitman ('19) refers to the fact that "behavior is of prime importance in sex recognition" and concludes that the behavior of the new comer, after the first encounter, is the only mark by which the courting males are informed about its sex.

If a visual cue, such as any of those found by Noble and Vogt in dimorphic birds, will function, an artificial situation might furnish some clue to it. The question will arise, of course, as to whether the results of experiments in such situations, being abnormal, are of significance. Tinbergen ('35), in his report on the behavior of the red-necked phalarope comments on this point. He says, "These aberrations (attempts to copulate with others, with lifeless things, etc.) of the sexual impulse have been observed especially in the case of captive birds, and it has often been said that they are 'abnormal' and nothing more and that they consequently are worthless for a real understanding of the psychology of birds. . . . I would on the contrary emphasize the importance, which these 'abnormal' cases have especially for psychology, as they show us the working of the inherited instinctive impulses under uncommon circumstances, and reveal in this way characters and features, which remain hidden in normal life." With such a purpose in mind as that to which Tinbergen refers, certain experiments were attempted. The object was to determine, if possible, if recognition in ring doves is in any measure based upon the visual cues of color of plumage and contour differences in individual birds (fig. 1).

In experiments with color, vegetable dyes, eosin, gentian violet and green were used. Breasts and tail feathers were colored. In the experiments with changes in contour, various alterations were made. In some birds, the plumage of the breasts was plucked so as to expose an area about one and one-half inches in diameter. Conversely, in others three cross rows of feathers, turned under side out so as to cause them to curl away from the body, were glued to the tips of breast feathers (fig. 1). The effect was one of puffed breasts with much ruffled plumage. In other birds, the tail feathers were plucked causing the birds to appear stultified and unbalanced (fig. 1). The opposite effect was secured in still others by adding an extra length of tail feathers (fig. 1). This was done by gluing the tail feathers removed from the preceding birds to the tips of the tail feathers growing in the latter. Duco cement was found effective for this purpose. The feathers so attached, remained in place for more than the eight day observation periods in a very

satisfactory manner. The birds in which either dyeing of plumage or contour changes were made, were removed from their cages and so treated at least a half hour before observations began. The alterations were made out of the sight of the flocks involved and the changed birds were then kept in isolation until needed. This permitted drying of colors or setting of glue, as the case might be, and allowed some time for such birds to become accustomed to their own changed plumage.

In 1935, some preliminary observations in which color of plumage was concerned, had been made. While too limited to be of much importance when considered alone, their results may be referred to here in connection with the more extended investigations in the later flocks. A normal, strange blond male; a strange, white male; and finally a familiar blond male and the

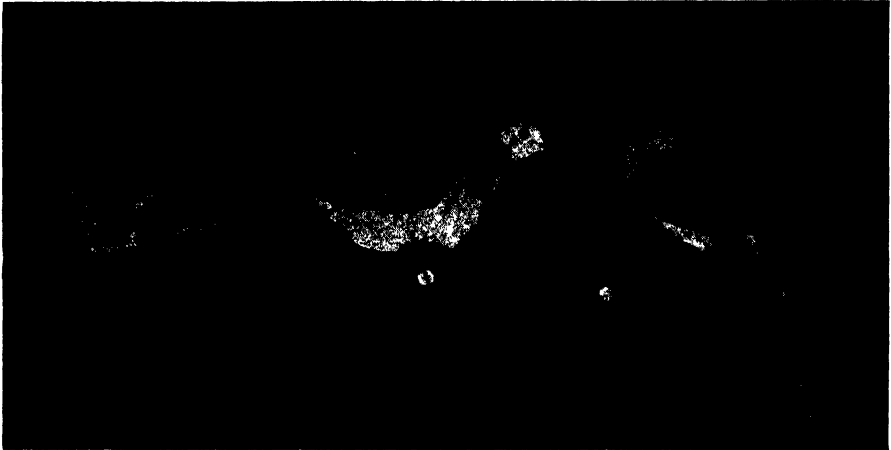


FIG. 1. Alterations in the contour of Ring Doves used in recognition experiments.

original normal, strange blond, each of the two latter dyed with picric acid, were introduced, one at a time into the male flock.

With the introduction of the white bird, a violent disturbance was the immediate reaction. For a brief period, the birds flew wildly about in what appeared to be a high degree of alarm. Then *RW* began courting the white dove and the flock returned to its usual behavior. In the evening the white bird was found sitting passively at the end of one perch, *RW* and *V* both courting him. The records of the contacts in both observation periods show the social organization to have been completely disrupted. *RD*, who previously had been consistently at the top of the hierarchy (table II), had but one pecking contact here, and *V*, who had previously remained subordinate to *RD* only, although engaging in 31 contacts with four other birds in the afternoon of this day, became subordinate to three. In the evening, *U*, who had been next to the lowest in rank in the afternoon, again assumed his

usual high rank, becoming dominant in four or five contact pairs. This indicates a temporary disturbance of social order rather than a permanent one.

When the strange blond was introduced, no alarm was apparent. That the birds were aware of his presence was indicated by the fact that they followed him about. Aside from *RW*, none showed a tendency to court him. In the evening, however, much courting was being done, 25 cases of mounting and six of billing occurring in a half hour. The strange bird's plumage was bedraggled and ragged and he appeared to be much the worse for wear when removed the following day. The flock organization was chiefly affected in that few contacts between old members occurred. The attention seemed to be centered on the strange bird. *RD*, who previously was not allowed to alight on the lower perch without setting up a violent series of pecking contacts, could now perch in this location with impunity.

A third experiment was made in the case of *WW*. He was removed from his flock, his plumage was stained with picric acid, and then allowed to dry for some hours. He was returned to his home cage just preceding the afternoon observation period. The remaining birds in the flock seemed more frightened than in the case when the white bird was introduced. They beat violently against the wire of the cage in attempted escape. All fled at *WW*'s approach. The latter behaved in his usual manner, apparently unaware of any irregularity. The period of seemingly intense fright was brief. After five minutes the violence had abated but *WW* was avoided for 16 minutes more. Then courting in the flock began and pecking was resumed. After 21 minutes the flock relationships seemed quite normal. In the evening observation period, fewer contacts than were ordinarily noted occurred but otherwise the flock as a whole seemed quite as usual. In this case, observations continued for a week but no further irregular behavior was noted.

The strange blond used in a preceding experiment and, subsequently completely isolated from the male flock, was stained as *WW* had been and reintroduced into the male flock. Again no alarm at his advent was observable except in a slight degree on the part of *WW*. This was in marked contrast to the effect of the white dove's or *WW*'s introduction. *RW* and *V* immediately began courting the strange bird. Soon *RD* joined them. The stranger withdrew to a perch, remaining there until vicious pecks, sufficient to draw blood, drove him off it. Immediately the other seven began courting him. In the evening and on the following day, the stranger was found in a corner on a perch, extremely submissive and apparently no longer noticed by the group. The flock organization for the observed periods was affected chiefly in a noticeable decrease in pecking contacts.

The results of these four brief experiments, the effect of introducing a strange white, a strange blond, a familiar blond dyed, and reintroducing the strange blond similarly dyed, indicate that a recognition of other birds of the same species, while superficially affected by appearance, must depend upon

other factors. Alarm seemed indicated in the case of the strange white dove, normally different in appearance. A strange bird, but one similar in coloration of plumage, appeared to arouse no alarm. The reaction was that accorded any strange blond ring dove as described by Whitman ('19), one of attempted sex contacts followed by pecking contacts. Even when dyed, the bird was treated similarly, a recognition of it as an intruder seemingly taking precedence over a response to it as an anomaly. The member of the flock artificially colored produced a very different reaction. Here it seems that the unusual appearance resulted in the temporary terrorization of the group. Had it been the reaction to the color, it would seem that a similar one would have occurred in the case of the strange dyed blond. Two explanations can be offered. The birds may have recognized *WW* and so not have reacted to him primarily as an intruder. It may be then that the alarm was due to an unusual change in a familiar individual. On the other hand, since the strange blond was dyed and introduced after a period of contact in the flock with *WW* similarly dyed, it is possible that such coloration on the part of any bird would no longer excite any terror. This idea is supported by the observation that *WW* alone showed evidence of alarm when the dyed strange blond was introduced. Since *WW* had been unable to get a complete view of himself, it may be that he reacted as the whole flock would have done

TABLE IX. *Order in peck-dominance in female flocks of ring doves A and B as affected by artificially colored plumage, 1936 and 1937*

Flock A		
Control	<i>WT</i> (Green)	<i>RR</i> (Green)
8 days		
<i>J, RR, RT, P</i> (2)	<i>J</i> (4)	<i>J, RR</i> (2½)
<i>O</i> (1)	<i>RR</i> (3½)	<i>RT, O</i> (2)
<i>II, WT</i> (0)	<i>RT, O</i> (2)	<i>WT, P</i> (1½)
	<i>WT, P</i> (1)	<i>H</i> (1)
	<i>II</i> (½)	
4 days		
	<i>J</i> (3)	<i>J</i> (3)
	<i>RR</i> (2½)	<i>RR</i> (2)
	<i>WT, P, O</i> (1)	<i>WT, P</i> (1½)
	<i>H</i> (½)	<i>H, O</i> (1)
	<i>RT</i> (0)	<i>RT</i> (0)
Flock B		
Control	<i>N</i> (Eosin)	<i>Y</i> (Eosin)
8 days		
<i>N, DD</i> (2)	<i>DD, Z, S</i> (3)	<i>M</i> (2½)
<i>S</i> (1½)	<i>M</i> (2)	<i>N, Z</i> (2)
<i>Y, M</i> (1)	<i>Y</i> (1)	<i>Y, DD, S</i> (½)
<i>Z</i> (½)	<i>N</i> (0)	
4 days		
	<i>DD, S</i> (2½)	<i>M</i> (2)
	<i>Z</i> (2)	<i>Y, N, Z</i> (1)
	<i>M</i> (½)	<i>DD, S</i> (0)
	<i>Y, N</i> (0)	

had this been the first, rather than the second bird, in the experience of the flock to have an unusual coloration.

In the flocks experimented with in the fall of 1936 and the winter following, where plumage was altered with vegetable dyes or in contour effects, records were kept for eight day periods. Since the preliminary work of 1935 suggested the possibility of unusual disturbances to be anticipated in the initial part of each period, it was decided to make four day summarizations also. This would bring into greater contrast marked temporary aberrations than would be the greater spread of eight days. Initial controls were established by making observations over eight day periods preceding experimental periods. Four groups designated as female and male flocks A and B were used. In tables IX and X are included the names of the dyed birds and the color used in each case. An attempt was made to use for coloring only birds occupying intermediate positions in the social organization of preceding periods. By this means, shifts either upward or downward could be noted. Such selections were not always practicable, however.

TABLE X. *Order in peck-dominance in male flocks of ring doves A and B as affected by artificially colored plumage, 1936 and 1937*

Flock A					
Control	RS (Eosin)	Control	RC (Green)	U (Green)	RD (Gentian)
8 days					
VV, TT (5)	RD (6)	RD (4½)	RD (4½)	RD, U (4)	RD (6)
RS (4)	VV, RC, RS (3½)	RS (3½)	U (3½)	RS (3½)	RS (4)
RC (3½)	TT (2½)	VV, RC (3)	V, RC (2½)	VV (3)	RC (3)
RD (2)	V (2)	TT, U (2½)	VV, RS (2)	TT, RC (2)	VV, TT, V (2)
V (1)	U (0)	V (2)	TT (0)	V (1½)	U (1)
U (½)					
4 days					
	TT (5)		RD (4½)	RD (6)	RS (3½)
	VV (4)		VV, U (4)	RS (3½)	RD (3)
	RC, RS (2½)		RS (3½)	VV (2)	V, RC (2½)
	V (2)		RC (2½)	V, RC (1½)	VV, TT (2)
	RD (1)		V (1½)	U (1)	U (½)
	U (0)		TT (0)	TT (½)	
Flock B					
Control	WG (Eosin)	D (Eosin)	G (Gentian)	Control	TR (Eosin)
8 days					
TR, G (5)	F (5½)	G, D (5)	G (5½)	G (6)	TR (5)
F (4)	S, G (4)	WG (4)	D (4)	TR, WG (4)	WG, G (4½)
WG, D (3)	TR (3½)	TR (3)	TR, F (3)	F, D (3)	F, D (3)
AA (1)	D (3)	F (2)	S (2½)	AA (1)	AA (1)
S (0)	WG, AA (½)	S, AA (0)	WG (2)	S (0)	S (0)
			AA (0)		
4 days					
	G (5½)	D (5)	G (4½)		WG, G (5½)
	D (4½)	G (4)	D (4)		TR, F, D (3)
	F (4)	WG (3)	WG (3)		AA (1)
	S (3)	F (2)	TR, F (2½)		S (0)
	TR (2)	TR (1)	S (½)		
	AA (1)	S, AA (0)	AA (0)		
	WG (0)				

On basis of the data summarized in tables IX and X, alteration in appearance due to coloration of plumage is not shown to materially affect the permanent organization of a flock. In female flock A, *RR*'s position was either in the first or second rank throughout the two preceding and the experimental periods, as well as in the initial four days of the latter. *WT* following coloration did rise from the lowest in the control observation period to an intermediate position in the first four days of the experimental one. She remained one rank above the lowest through the whole eight day period. In female flock B, *N* after dyeing, dropped from highest in the control to lowest in the experimental period and then rose to an intermediate position in the subsequent period. Under similar circumstances *Y* changed one place.

In the male flock A, no change was evident in *RS*'s or *RC*'s positions after dyeing them; a drop of one place only occurred in the four day period with *RD*. In the 16 days preceding coloration, *U* had rather rapidly ascended in rank from lowest to the next highest rank. He dropped to next lowest in the first four days after dyeing, only to rise before the eight days ended to the highest rank. This rise could not have been entirely due to the color, as subsequent to this, *U* made a descent to lowest place in the next eight day period. In male flock B, *WG* made a marked descent in rank following coloration. This was followed by a rapid return to his previous status. This, as in the case of *U*, is not as significant as it first appears, since this bird (*WG*) made another rapid descent and rise 16 days later. *D* made a rather marked rise, falling again later to his former low rank. *TR* ascended one place in rank.

Since changes in rank in the flock are quite common in ring doves, it may be that changes in rank during the experiments in colorations are fully explained on that ground. Nevertheless it is to be noted in all but one of the 12 cases, that some change in rank did occur. In six, 50 per cent, the change in the four day period was greater than in the eight, as contrasted with a greater change in 25 per cent during the eight day period. In two the change was the same for the eight as for the four day period. With the birds not colored, 23.3 per cent showed a greater change in the eight day period than the four day and 26.6 per cent in the four day period than in the eight day. Twenty per cent showed no change. The greater proportion showing changes in rank among the colored than with the uncolored doves and especially in the four day period, suggests that the change in appearance may have had some effect on the social organization, even if a temporary one.

The behavior of the doves on the reintroduction of the dyed individuals was closely observed. Certain stages in recognition were noted to occur, though in varying degrees.

1. Either alarm, with active withdrawal from the proximity of the colored bird or a marked pause in the usual activity without withdrawal was noticeable.

2. The second stage was quite similar to the usual initial reception of a new comer of the same species, an approach on the part of some or all the birds. It differed in that frequently the birds paused as if bewildered at some inexplicable change.

3. Courting of the colored bird by the members of the flock followed the approach. This courting was particularly noticeable as it occurred in the case of several dyed birds which no other birds had previously been observed to court.

The unusual sexual excitement which the coloring seemed to stimulate was the most striking feature of this period. In birds in which dimorphism is not exhibited and in whose plumage no bright or especially deep shades of color are found, it seems strange that artificial changes in color of plumage should so stimulate sexual behavior. When entirely strange birds were introduced, colored or uncolored, there was little or no initial alarm or apparent bewilderment. In such cases, the immediate procedure was that of attack, combined with courting. In most cases such birds were subdued within a few hours and driven into retirement on the end of some perch. With the colored birds, removed only the short time involved in dyeing and drying, the courting differed from that with strange birds in not being accompanied by pecking. This was noticeable with contact pairs, previously in very frequent combat.

It seems reasonable to conclude on basis of the data obtained from observation of flocks in which one member was dyed in a very conspicuous manner, that the social organization is temporarily affected in some degree by the reactions to the new situation. This change in organization appears to be of short duration but to be marked while it lasts. Therefore, while color may be a factor in recognition, it seems to be very limited in effects on continued flock organization.

A factor entering into visual recognition of individuals by man is that of contour. Several experiments were devised to determine, if possible, whether ring doves show such recognition. If so, in how far is social organization affected by it? Seven experiments were performed, two with females, five with males. (The results of three other experiments with females were discarded when a male was found to be a member of the flock.)

Few marked changes in hierarchy (tables XI and XII) were observed during this series of contour alterations. As with those with color, the changes which were noted may have been the result of normal fluctuations in the social order within flocks. No violent disturbances immediately followed the entrance of any altered bird. Hence less temporary disorganization occurred in the four day period in contour changes than in those with color. The only marked change in rank was in *V*, the male to whom breast plumage was added. There was a descent here from highest to lowest rank in the four day period. *V*'s course in preceding periods was an erratic one, hence

TABLE XI. *Order in peck-dominance in female flock A of ring doves as affected by artificially altered contour, 1937*

Control	WT (Plucked tail)	J (Added tail)
	8 days	
J, RT (4)	RT (4½)	RR (4)
RR, P, O (3)	J (3)	RT, P, O (3)
H, WT (1)	WT, P (2)	J (2)
	H (1)	H, WT (1)
	O (½)	
	RR (0)	
	4 days	
	J (3)	J, RT, O (2)
	P (2)	H, WT, P (1)
	H, RT, WT, O (1)	RR (0)
	RR (0)	

TABLE XII. *Order in peck-dominance in male flocks A and B of ring doves as affected by artificially altered contour, 1936 and 1937*

Flock A					
Control	V (Plucked tail)	RS (Extended tail)	RD (Plucked breast)	Control	V (Added breast plumage)
	8 days				
TT (7)	VV, TT (5½)	TT (7)	TT (5½)	V (5)	VV, TT (5)
RS (6)	RD (4)	RC (5)	VV, RS (5)	VV, TT, RC (4)	RS (4)
RD (5)	U (3½)	RS (4½)	V, RC (4)	RS (3)	RC (3½)
VV (3½)	V, RS (3)	VV (4)	RD, U (2)	RD (1)	RD (2)
V (3)	D (2)	RD (3)	D (½)	U (0)	V (1)
U (2)	RC (1½)	U, V, D (1½)			U (½)
RC (1½)					
D (0)					
	4 days				
	RD, VV, TT (5½)	TT (5½)	TT (7)		VV (5)
	U, V, RS (4)	RD (4½)	RS (5)		TT (4)
	D (1)	VV (3½)	RC (4½)		RS (3)
	RC (0)	D (2½)	VV (4)		RD, RC (2)
		RC, U, RS (2)	V (3)		U, V (1)
		V (0)	RD, U (2)		
			D (½)		
Flock B					
Control	G (Added breast plumage)				
	8 days				
G, F (5)	TR, G (5½)				
TR (4)	F, D (3½)				
AA (3)	WG (2)				
WG (1½)	AA (1)				
D (1)	S (0)				
S (½)					
	4 days				
	TR, G (5)				
	F (3)				
	WG, D (2)				
	S (1)				
	AA (0)				

it is not unreasonable to explain his abrupt change here as one characteristic for him under any circumstances.

The behavior in the flocks undergoing color alterations was found to be temporarily affected. No such disturbance was observable in connection

with contour changes. In *V*'s case only did a flock give evidence of any immediate recognition of alteration. No alarm was evinced but the birds did gather about *V* and look at him about ten minutes. Then in a marked degree, they began courting him. As was to be expected, the altered birds, themselves, were much disturbed by losses or additions of plumage, particularly the latter. That flaunting added parts would attract attention and prove disquieting to the others seemed probable. It was not found, however, that this was noticed by other birds, unless momentarily in a few cases.

On basis of the observations and the data obtained regarding contour, we may conclude that contour is of very minor importance in recognition and in the establishment of the social hierarchy. Evidently the members of a flock depend upon other factors for recognition. Moreover, they seem not to be confused in identities, at least to any marked degree, by such alterations as loss or addition of tail feathers and breast plumage.

Experiments with alteration of color and contour have not satisfactorily solved the problem of recognition in flocks of ring doves. These birds evidently notice changes produced by adding color. This is to be expected from studies made of their powers of vision. These show them to have much the same sensitiveness to wave length as does man and to have a similar tri-chromatic mechanism and "line discrimination curve" (Hamilton and Coleman, '33). The initial reactions to the colors noted, which seem to be fright and perplexity, appear to be those evoked by an abnormal situation. It seems that only when some factor or factors, concerned with behavior, become apparent to the bird, does recognition occur. In the case of contour, the changes seem ones of small moment in a ring dove's life. It may be, for example, that an abbreviated tail in a dove is too common an occurrence to excite any reaction. Young birds' tails are abbreviated, and older birds frequently lose tail feathers. It is difficult to explain why the extenuated tail, and the display made by its unfortunate possessor, did not attract greater attention. If the explanation of recognition is to be satisfactorily made, it will have to be on some other basis than that of visual cues of color and contour as used in the present study.

DISCUSSION

There seems little argument as to the existence of a definite social hierarchy in ring doves. The order is quite similar to that observed in the common pigeon. This is to be expected in birds as closely related as these species of the Columbidae. Recognition between the individuals of a ring dove flock is evident. The basis of this is seemingly some more subtle factor or factors than gross color or contour peculiarities. The evidence is in favor of an explanation on the basis of recognition, visual and auditory, having primarily to do with behavior. Investigation having to do with modification of innate factors in behavior seems more promising as a means of explaining

the social relationship of the flock members than that with changes in gross appearance.

The tabulations used in this study are based on 10,915 pecking contacts during 273 hours. In each of these one or the other of the birds in the pair involved was successful. Many "non-decision" contacts observed are not included. The average per hour of the tabulated contacts was 39.9 for all birds. In female flocks these contacts averaged 20.1 per hour, in the male flocks, 53.8 per hour. Frequently the combats were vicious; in a few blood was drawn. The observations reported in this study were supplemented and confirmed by ones in a larger outdoor pen, by those of other caged groups of varying numbers, young and old, heterosexual and homosexual, and by those of paired birds. They tend to discredit the expression "gentle as a dove" and to raise a question as to the suitability of the dove as an emblem of peace.

CONCLUSIONS

1. A peck-dominance, rather than a peck-right, determines the social organization of caged flocks of ring doves.
2. Recognition of change in appearance of ring doves, due to artificial coloration of plumage, is evident in a tendency toward a temporary disturbance of the social order, accompanied by certain peculiar aberrations in general behavior.
3. Recognition of change in appearance in ring doves, due to artificial alteration in contour, is evident in a very limited degree. The social organization shows no unusual modification.
4. The evidence indicates that differences in color or contour are not factors of any considerable importance in recognition of individuals in flocks of ring doves.

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A PHYTOSOCIOLOGICAL ANALYSIS OF A TUPELO GUM FOREST NEAR HUNTSVILLE, ALABAMA

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Tupelo gum forests in the United States are numerous along the seaward margin of the coastal plain from Texas to Virginia. In addition, many stands occur in the alluvial flood plains throughout the Southeastern States. The community is designated as Cover Type Number 95 by the Committee on Forest Types of the Society of American Foresters. In the Committee's report on "Forest Cover Types of the Eastern United States" (1932), the tupelo gum forest is described as being composed of tupelo gum, *Nyssa aquatica*, in pure stand, or tupelo gum predominating with the following associates: southern cypress, *Taxodium distichum*, red maple, *Acer drummondii*, swamp black gum, *Nyssa biflora*, pumpkin ash, *Fraxinus profunda*, and, in the north, water ash, *F. caroliniana*. Variants of Cover Type Number 95 are listed as sweet bay-swamp black gum, and southern cypress-tupelo gum forests, the name of the variants depending upon the species present. This forest cover type and its variants are of much importance because of the great density of the stands and the extensive areas they cover.

A pure stand of tupelo gum, some seven miles south of Huntsville, Alabama, was analyzed in July, 1938 (fig. 1). This swamp is included in the tract of land owned by the Byrd Spring Rod and Gun Club. It has an area of about 600 acres, and is referred to as Byrd Spring Bottoms by all who are well acquainted with the area. The swamp lies in an elongated basin which is continuously wet due to a spring-fed stream which meanders through it.

The forest floor is intricately designed with numerous snail tracings on the soft surface of the oozy mud. And in the shallow water, muddy streaks betray the movements of fish which are disturbed by the investigator as he proceeds on the fisherman's walkway, or sloshes through the swamp. The trees are tall, with few branches, and clothed on the north faces with dark green mats of liverworts and mosses. These mats are especially dense on the swollen bases of the tupelo gum which extend from the ground level up as high as a man's head. In general, one sinks halfway to the knees as he attempts to proceed through the swamp, but in several places, he sinks nearly to the hips and progress is quite impossible. This difficulty has been circumvented by the members of the Byrd Spring Rod and Gun Club by the construction of a walkway, 18 to 24 inches above the forest floor.

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Nyssa aquatica ² is the predominant species of this swamp forest. It is characterized by swollen bases and occasional knees or looping roots. In this stand, however, there were only twenty knees per acre as against two to four hundred in similar communities in Mississippi and Louisiana. The trees are devoid of branches except for the upper third of their height and many of the tall, barren trunks are peculiarly arched to the south (fig. 2). The trees average 104 feet in height and 9.0 inches in diameter above the enlarged bases. The swollen butts, however, attain an average diameter of 16.5 inches.



FIG. 1. General view of tupelo gum showing smartweed invading shallow flats along the stream margin.

The age of the trees was not determined but ring counts of felled tupelo gum trees in neighboring swamps indicate an average annual increment of about 0.13 inch. On this basis the mature trees would approximate 200 years of age. The general appearance of the trunks is dark green from the north, as contrasted to a light gray when viewed from the opposite direction. This is due to the absence of bryophytes on the south side of the trunks, although several lichens are evident. In spite of the existing hydric conditions, appar-

² The "Manual of the Southeastern Flora" by Small (1933) has been closely followed in nomenclature.

ently the humidity of the air is not great enough to provide the minimum water requirements of bryophytic associations on the southern exposure. On the other hand, the north surfaces of the trunks are heavily clad with creeping



FIG. 2. Interior of tupelo gum swamp showing walkway, leaning trees and sparse herbaceous understory.

communities of mosses and liverworts, and even an occasional settlement of the fern, *Polypodium polypodioides*.

Arborescent synusia. The well-developed arborescent synusia was analyzed by staking out ten consecutive quadrats of 100 square meters each (ap-

proximately 1/40 acre). The stand investigated is apparently of uneven age, and hence the quadrat line was selected in such a manner that all age classes existing therein would be sampled. Only two arborescent species, tupelo gum and red maple, occurred in the quadrats and only the former species is of importance. Individuals of each species were separated into those greater than one inch in diameter just above swollen base; and those less than one inch. In the larger size class, tupelo gum averaged 652 living trees per acre with an average D.B.H. of 9 inches; in addition, 44 remnants of trees, which were represented by stumps or snags, were observed. In the smaller size class 276 individuals of the tupelo gum were recorded for each acre. The density of red maple was very low, only 32 individuals of the larger size class were encountered, and their average diameter was less than 2 inches, hence the red maple is not a significant component of the community.

A comparison of the basal areas of the two species illustrates more convincingly the minor role played by this latter species. The basal area of tupelo gum at the bottleneck was 233 square feet per acre as contrasted to 0.5 square foot for the red maple. The basal area of tupelo gum through the swollen butts (1 foot up) was 981 square feet, slightly more than four times that found at the bottleneck. These data compare closely with those of a swamp black gum forest of uniform age in which the basal area ratio (swollen butt: bottleneck) was found to be slightly more than 3:1.

A careful reconnaissance of the stand for trees, shrubs, and vines revealed a total of twelve woody species, eleven of which play a very subordinate role to tupelo gum in the composition of the community. Tupelo gum and red maple are found distributed throughout the swamp. Buttonball bush, *Cephalanthus occidentalis*, green ash, *Fraxinus pennsylvanica*, and virginia willow, *Itea virginica*, are rarely encountered and are found only where the forest floor is elevated two to six inches above the mean soil surface. In similar situations, near the periphery of the swamp, the pretty swamp rose, *Rosa palustris*, was observed as was also an interesting legume, *Amorpha fruticosa*. The climbing hydrangea, *Decumaria barbara*, and poison ivy, *Toxicodendron radicans*, are conspicuously outlined against the tupelo gum trunks, although neither is abundant. Swamp loosestrife, *Decodon verticillatus*, closely entwined by the hemp vine, *Mikania scandens*, occurs in dense patches 100 feet or more in diameter where the crown cover is low or absent. The patches are found in saucer like depressions, four to six inches below the average level of the swamp floor.

Growth of the deciduous forests in the Tennessee Valley begins by the middle of March. However, it is early April before the tupelo gum forest is well in leaf. In late June the fruits are reaching maturity at which time many seeds from last year's crop have just completed germination. Establishment of the seedlings occurs mainly on the higher elevations of the swamp floor. Approximately 1300 young tupelo trees less than one inch D.B.H. were found per acre in areas where the soil level was 2 to 4 inches above the average

soil surface of the swamp as contrasted to only 80 young individuals of the same species on the normal swamp floor.

Herbaceous synusia. The old growth tupelo gum swamp, apparently characteristic of all primeval stands, possesses a very poorly developed herbaceous understory. This is in striking contrast to the cut-over cypress-gum swamp described by Penfound and Hathaway ('38). At the most, the herbaceous synusia is ill defined, and a quadrat analysis of this stratum was deemed inadvisable. However, the species present were listed in two groups. Typical swamp species which occur floating on the water or rooted in the



FIG. 3. Interior of tupelo gum swamp showing relatively dense stand of lizard's tail on a slightly elevated portion of the forest floor.

substratum of the swamp proper include: *Ceratophyllum demersum*, *Didiplis diandra*, *Isnardia palustris*, *Lemna minor*, *Proserpinaca palustris*, *Saururus cernuus*, and *Sisymbrium nasturtium-aquaticum*. The most important of these, the lizard's tail, *Saururus cernuus*, and the buttonweed, *Didiplis diandra*, exhibit a high degree of sociability but occur in localized patches, the former on somewhat elevated areas (fig. 3) and the latter along the edge of a narrow channel 4 to 6 inches below the average soil level.

A second group of marginal species occur on logs, tree trunks, or on unusually elevated portions of the forest floor. They include *Bidens* spp., *Boehmeria cylindrica*, *Carex aspera-grayi*, *C. decumbens*, *Lycopus rubellus*, *Persicaria portoricensis*, *P. setacea*, and *Triadenum petiolatum*.

Physical factors. The crown cover of the swamp, as based on estimates of three observers, was placed at 75 per cent. The dense canopy was also determined by estimating the amount of shade cast on the forest floor at high noon, as against the aggregate area of light flecks. Fifteen temporary quadrats of one square meter each were selected at an arbitrary distance of four paces apart, and the percentage of shade in each quadrat was estimated. Although the percentage of shade varied greatly in the quadrats (30 per cent to 100 per cent), it is believed that the average figure of 81 per cent represents effective coverage very well, since it takes into consideration the shade cast by the trunks and branches, as well as that by the leaves. Readings on a Weston Foot Candle Meter were made throughout the community, except for light flecks which could not be recorded on the instrument (Max., 600). An average of 150 (40 to 300) foot candles was obtained. This shade is sufficient to exclude practically all herbaceous vegetation, as is supported by the increase in number of species and individuals wherever the canopy is opened.

The slightly alkaline surface water (pH 7.1) covers the forest floor approximately nine months of the year. During most of August, September, and October the water is confined to the narrow channel which meanders through the swamp. The maximum height of the annual water cycle is usually reached in March at which time the surface water may be 30 or more inches in depth. The average depth of water on the forest floor is estimated at 4 inches. The extended hydroperiod and the dense cover with which it is associated account for the paucity of herbaceous species.

The water holding capacity of the soils was determined for samples which were collected from the first, second, and third foot horizons of the swamp floor. To a depth of one foot myriads of rootlets of the tupelo gum were noted and very little soil was present. Here, footing is insecure and one often sinks through the matted mass of rootlets through several inches of ooze to the firmer soil below. Soil samples from the second foot horizon showed approximately a 50 per cent decrease in tupelo rootlets and a marked increase in organic matter. At the third foot level the rootlets were mostly absent, and to the unaided eye, the samples appeared to be composed entirely of decaying organic matter. The highest water content was found in the first foot of soil (652 per cent of dry weight) and below this level a gradual decrease was noted. The second foot level contained 430 per cent as contrasted to 279 per cent for the samples secured from the third foot horizon.

TABLE I. *Water content of saturated soil, tupelo gum swamp*
All figures in per cent of dry weight of soil

	Sample 1	Sample 2	Sample 3	Average
First Foot	483.3	606.5	865.7	651.7
Second Foot	475.3	533.3	280.8	429.8
Third Foot	308.9	286.4	242.6	279.3

Biotic factors. Byrd Spring Bottoms is a hunters' and fishermen's paradise and is frequented often by members of the club. Utmost respect is held by members for the wild life of the area, and a deputy is present to help conserve the interesting fauna and flora found therein. No evidence of fire in the recent past was present, and practically no cutting has occurred, nor is any anticipated. In the interest of conserving the water supply, a small dam has been constructed near the upper end of the swamp. Flash boards about ten inches high, and with openings between, allow the water levels on either side of the dam to approach each other during periods of low flow. In June the water level above the dam was noted as being 14 inches higher than that below. In the upper part of the swamp where the water has been raised and held above the original high water level for long periods, young tupelo gum, as well as several other woody species, have been killed. Undoubtedly, this small imbalance has been compensated for, since the dam has provided environmental conditions which are conducive to the production and perpetuation of fishes and other wild life. Below the dam normal conditions are encountered and only this part of the stand was subjected to investigation. It is believed that man's efforts have exerted little or no influence on the vegetation below the dam, and also, that the data herein reported are representative of the virgin tupelo gum forest.

Tupelo gum swamps, generally, have been favorable to the breeding of anopheline mosquitoes. When these swamps are cleared a profusion of woody shoots are produced and a considerable number of aquatic herbaceous species invade the area. This condition is probably even more favorable to the production of malaria mosquitoes. Studies have been inaugurated in this and other swamps to determine the relative breeding in such areas and to ascertain, if possible, the relation of shade to anopheline breeding. These observations should be completed by the end of the 1939 growing season and the results will be reported by the entomologists of the Tennessee Valley Authority.

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STUDIES IN POPULATION PHYSIOLOGY. IX. THE EFFECT
OF IMAGO POPULATION DENSITY ON THE DURATION
OF THE LARVAL AND PUPAL STAGES OF
TRIBOLIUM CONFUSUM DUVAL¹

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INTRODUCTION

It has been shown in a recent study (Park, '38) that certain aspects of the post-embryonic development of the flour beetle, *Tribolium confusum*, are noticeably affected by crowding the larvae in a constant sized volume of flour. For example, if a series of cultures are established in which the number of larvae are varied from one to 256 individuals per bottle the forms die at a higher rate and pass through their metamorphosis more slowly as their densities increase. This phenomenon was demonstrated to obtain only if the medium was not changed or altered during the period of metamorphosis. When the flour was renewed at 48 hour intervals the crowding effect was dispelled; the larvae developed essentially as rapidly at high as at low population densities. From these data the conclusion was reached that the principal density effects noted were due, not to unique behavior interactions between the larvae themselves, but to the influence the larvae exerted on their environment. The ecologic implications of such density relationships have been discussed by Park ('37; '39).

In the analysis of population phenomena it is obviously necessary at times to set up experiments that possess a certain artificiality. This procedure seems justifiable if forthcoming results aid in the interpretation of population dynamics. Thus, in the experiments summarized above, it is patent that an unmolested culture of *Tribolium* would rarely exist as a strictly larval population. Nevertheless, the knowledge that larval density is related to larval and pupal development is of value in appraising the mechanics of the complete population. The experiments reported in this paper are also subject to a similar type of criticism but are presented in the light that the results have significance in the understanding of the natural population.

In a *Tribolium* population the biotic components are eggs, larvae, pupae and imagoes. Typically, all these stages exist together in any one population for any moment of time. The thing that changes with age is the numerical frequency or density of these components. It is important, therefore, to

¹ The present investigation was aided in part by a grant to the University of Chicago from the Rockefeller Foundation.

evaluate as far as possible the effect of any one population component upon any other. The present paper is concerned with the relation between imaginal population density and the rate of development of the larval and pupal instars.

To attack this point, experiments were set up in which certain elements of the environment—light, temperature, volume and kind of flour—were controlled as far as possible. All experiments were run in shell vials containing 8 grams of white flour. The vials were kept in a darkened incubator at a mean temperature of 29.2° ($\pm 0.8^{\circ}$) Centigrade. Into each of these standard vials were introduced 10 first instar *Tribolium* larvae that had just hatched. The larvae were selected at random from a closely in-bred stock culture. These larval populations were then supplied with imago beetles in such a way as to create the following five experimental series:

- Series A: 10 bottles; 10 larvae per bottle; 1 imago per bottle.
- Series B: 10 bottles; 10 larvae per bottle; 4 imagoes per bottle.
- Series C: 10 bottles; 10 larvae per bottle; 16 imagoes per bottle.
- Series D: 10 bottles; 10 larvae per bottle; 32 imagoes per bottle.
- Series E: 5 bottles; 10 larvae per bottle; 64 imagoes per bottle.

Each bottle was examined at 5 day intervals and dead larvae or imagoes were removed and replaced by beetles in a comparable stage of development. The replacement was made possible by running duplicate bottles for all series and drawing upon these when more forms were required. Thus, the initial densities were maintained during the tenure of the experiment. As the larvae approached pupation they were examined at 12 hour intervals. This permitted the larval metamorphosis to be timed to the nearest half-day. As pupae formed they were removed, sexed (Park, '34) and isolated singly into vials containing two grams of fresh flour. The pupae were not disturbed during their development. The emergence of imagoes was noted and also timed to the nearest 12 hour period. This span, from pupation to emergence, was taken as the duration of the pupal period just as the span, from hatching to pupation, timed larval development. In these experiments the density differentials were broken up at 30 days by placing the remaining larvae (never over 25) in 100 grams of fresh flour. This obviously accelerated pupation. All results discussed are based, therefore, on 30 days of crowding. The larval period was limited in this fashion because (1) it was thought desirable to have density operate over a constant time for all series and (2) it prevented the more crowded cultures, especially D and E, from lengthening their metamorphosis excessively.

The entire investigation attempts to control obvious physical factors and assay the effect of a differential imago density upon post-embryonic development. The two biological responses dealt with are the duration of the larval and the pupal stage. In a sense this is a study of rate of growth and it is believed that these rates are of importance in an understanding of population dynamics; *vide post.*

EXPERIMENTAL RESULTS

Duration of the Larval Period:—A statistical summary of the data describing the rate of larval development appears in Table I. In this protocol

TABLE I. *Statistical constants for the duration of the larval period*

Series	Range		Mean Length of the Larval Period (days)	Standard Deviation (days)	Coefficient of Variability (per cent)	n
	Maximum (days)	Minimum (days)				
A	29.5	19.5	24.5±0.074	1.11±0.052	4.5±0.214	100
B	37.5	19.5	25.4±0.127	1.89±0.089	7.4±0.354	100
C	36.0	24.5	25.4±0.113	1.64±0.079	6.5±0.316	95
D	35.0	24.5	28.3±0.322	4.40±0.277	15.5±0.802	85
E	46.0	29.5	33.2±0.332	3.31±0.234	9.9±0.700	45

the range of variation, the mean length of the larval period, the standard deviation of the distribution and the coefficient of variability are presented. Since the variation is small, the best way to appreciate the trend of the data is to examine the means. From even casual inspection it is apparent that, as the imaginal population density increases, the duration of the larval period increases. This can be visualized by setting up a table of mean differences between the various series as follows:

Series Subtractions	B-A	C-A	D-A	E-A	C-B	D-B	E-B	D-C	E-C	E-D
Mean Difference (days)	0.9	0.9	3.8	8.7	0.0	2.9	7.8	2.9	7.8	4.9

All these differences are significant statistically² except that existing between Series B and C. In short, it is possible within the limits of this experiment to lengthen the larval period of a constant sized larval population by increasing the number of imagoes with which those larvae live. These results are essentially like those described earlier (Park, '38) where only the larval densities were varied. The explanation, in all probability, is also similar. It is not primarily the effect the imagoes have directly on the larvae that alters the rate of metamorphosis, but, rather, the influence the imagoes exert on the flour. It has been shown in a number of earlier reports (for summary, see Park and Woollcott, '37) that imago *Tribolium* "condition" or biologically alter their flour by living and breeding in it. Thus "conditioned flour" is a "population product." As the *Tribolium* culture grows the flour becomes more conditioned; its nutritive value is lowered and it acquires metabolic waste products of various types as well as frass. Experimental analyses have shown that a number of responses—fecundity, larval and pupal mortality, rate of larval development—can be affected adversely by subjecting the beetles to conditioned flour. The lengthening of the larval

² Measured in the conventional way by calculating the ratio of the difference between any two uncorrelated means to the probable error of that difference.

period due to increased imago density indubitably means that the flour is being conditioned more rapidly in the heavier populations. In Series E, for example, the conditioning is more drastic than in D with consequent effect on the larvae.

There is some tendency for the length of the larval period to be more variable in Series D and E than in A, B, and C. This shows up especially when the standard deviations are compared. These differences, however, are not striking and do not warrant emphasis at the moment.

At every five day examination the ten larvae from each bottle were weighed as groups on an analytical balance to the nearest tenth of a milligram. These growth data are of interest in connection with the duration of the larval period. Before the experiments were started 100 newly emerged larvae were found to weigh 3.1 milligrams. Thus the mean weight per group of ten can be taken as 0.31 milligrams; a standard from which all series start. In Table II the mean weight of ten larvae for all populations of Series A,

TABLE II. *Mean Larval Growth in Weight*

Series	5 Days (mg)	10 Days (mg)	15 Days (mg)	20 Days (mg)	25 Days (mg)
A	0.63	3.91	15.12	28.08	—
B	0.65	3.39	12.82	25.97	—
C	0.70	3.82	12.02	25.46	—
D	0.61	2.79	9.52	20.86	26.47
E	0.64	2.04	6.86	14.71	22.90

B, C, D and E is given relative to the age of the population. This increase in weight is an index of the average growth. These data are graphed in figure 1 where the abscissa is time and the ordinate is mean larval weight. The abscissal coördinate is an arithmetic scale and the ordinate is a logarithmic scale. The curves are smoothed but not fitted to any particular function.

It is apparent from the table and the figure that the rate of larval growth in terms of weight is correlated with imaginal density. The larvae of Series A, B and C grow rapidly and reach about the same mean weight at 20 days. There is the suggestion that the A-larvae are growing faster than B- and C-larvae. This, of course, corroborates the data of Table I. The larvae of Series D and E grow more slowly but eventually attain a weight not unlike that of the less-crowded cultures. The E-larvae, as anticipated, are adding weight at a slower increment than the D-larvae. It is interesting to note that the curves shown in figure 1 are all of the same general form. This suggests that the density differentials do not affect the basic pattern of growth. In general, the weight data seem to support the larval duration data rather adequately.

Duration of the Pupal Period:—It will be remembered that the length of the pupal stage, as well as length of the larval period, was determined for all series. These data are summarized in Table III. The re-

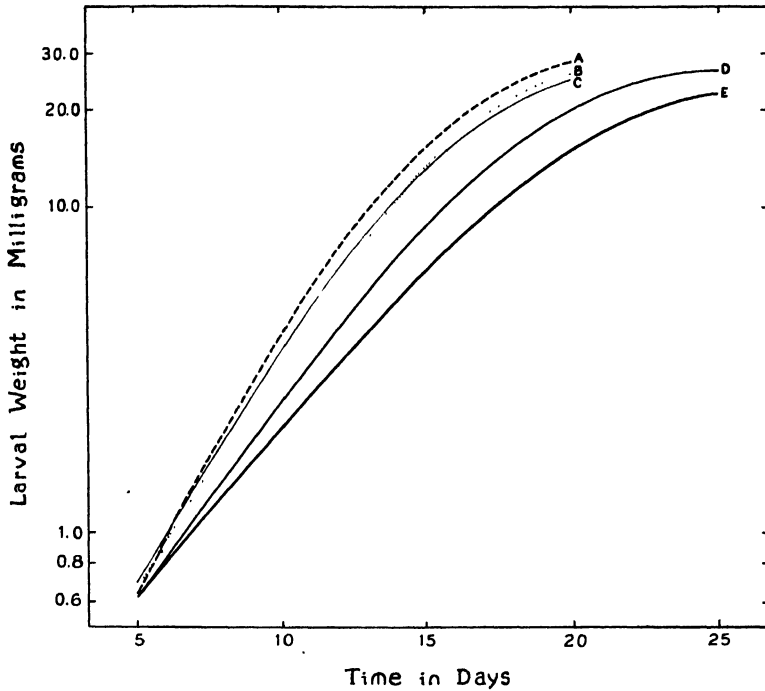


FIG. 1. Growth in weight of 10 *Tribolium* larvae reared under 5 conditions of imaginal density.

TABLE III. Statistical constants for duration of the pupal period

Series	Range		Mean Length of the Pupal Period (days)	Standard Deviation (days)	Coefficient of Variability (per cent)	n
	Maximum (days)	Minimum (days)				
A	7.5	5.5	6.52 ± 0.029	0.50 ± 0.020	7.7 ± 0.320	131
B	8.0	4.5	6.86 ± 0.033	0.57 ± 0.023	8.3 ± 0.370	129
C	8.0	3.5	6.60 ± 0.036	0.61 ± 0.025	9.2 ± 0.386	129
D	8.0	3.0	6.89 ± 0.036	0.61 ± 0.025	6.8 ± 0.290	125
E	8.0	5.0	6.75 ± 0.059	0.76 ± 0.041	11.3 ± 0.626	74

sults can be interpreted by study of the means. There is no consistent effect of imaginal density on pupal duration. If the means of Series A, B and C are grouped to form a single mean (6.66 days) and this compared with the mean of Series D + E (6.82 days) the difference is not significant relative to its probable error. In short, pupae develop essentially as rapidly if they were associated as larvae with 64 *Tribolium* imagoes as they do if they were associated with one or four imagoes. This experience was duplicated in earlier experiments (Park, '38) where only larval

density varied. There, the pupae were segregated according to sex as well as density and it was shown that neither of these factors influenced the rate of pupal development. Biologically, the pupal stage seems much less labile than the larval stage. The latter is more readily affected by environmental factors. This is an important datum to appreciate from the viewpoint of population dynamics. It suggests that the population is more moulded and altered, in one direction or another, by its larval than by its pupal components.

The standard deviation and the coefficient of variability shown in Table III do not indicate that variation in the pupal period is greatly correlated with imaginal density. These parameters are all of the same general magnitude although Series E exhibits more scatter about the mean than any of the others. The significance of this, if any, is not apparent.

Analysis of Variance:—It is often the experience of the population biologist that no matter how similarly two populations are set up one culture may differ significantly from another in respect of a certain response. The explanation of this fact is frequently obscure; indeed the fact is not always recognized. In dealing with population statistics it is usually desirable to work with one figure that represents the trend of a series of data collected from sources that are as homogeneous as possible. This was the procedure of the present study where the mean was used in interpreting the results. It is also important to measure the dispersal of the observations about their mean as indexed by the standard deviation and the coefficient of variability. However, these constants group all the variation into one category rather than break it down into component parts. For example, in the present study no attention has been paid to the differences between individual bottles or cultures. It might prove interesting to examine these intra-series differences by applying the Analysis of Variance technique (Fisher, '33) to some of the material already discussed.

For any experimental series, say Series C, and for either duration of the larval or the pupal period, we can think of the variability (variance) in three ways: total, variation between means of populations and variation within populations. The *total variation* is the gross variation of the entire sample. The *variation between means* of populations signifies that part of the total variance due to differences between the ten individual bottles. The *variation within populations* represents an average of the variance within the ten bottles. If the variance "within" and "between" bottles is not significantly different the entire series is a homogeneous one. In other words, bottle 1 of Series C does not differ greatly from bottle 2 or bottle 7 and the experiment has been set up so that each bottle is a statistical counterpart of its fellow. On the other hand, if the variance "within" and "between" bottles does differ significantly, i.e., if the means for the individual populations differ significantly among themselves, the experiment is not ideally homogeneous.

This technique has been applied to all series of the present investigation for both larval and pupal duration. In addition, to broaden the experience,

other cultures of a different nature were set up. The latter consisted of the following bottles:

Series α : 3 bottles: 64 larvae per bottle; no imagoes

Series β : 3 bottles: 128 larvae per bottle; no imagoes

These populations were examined at 15 and 30 day intervals; the larval and pupal periods were timed to the nearest half-day; replacements were made to keep the densities up to their initial value, and the flour was not removed or altered during the 30 day tenure. The cultures were kept in shell vials containing four grams of white flour and run under controlled environmental conditions. No imagoes were present in these cultures; the density differences between α and β are due only to differences in larval numbers.

The actual analysis of the data and the method used need not be detailed here. The technique is fully discussed by Snedecor ('34). The results of the analysis are summarized in Table IV where the probability (in per cent)

TABLE IV. *Analysis of variance*

Series	Probability (per cent)
α -Larval	<1
α -Pupal	>5
β -Larval	<1
β -Pupal	5-1
A-Larval	<1
A-Pupal	>5
B-Larval	>5
B-Pupal	>5
C-Larval	>5
C-Pupal	>5
D-Larval	>5
D-Pupal	5-1
E-Larval	<1
E-Pupal	>5

that the variance *within* the populations of any one series differs significantly from the variance *between* the populations of the same series is recorded. A probability greater than 5 per cent² is usually, but arbitrarily, considered not significant—the entire series is a homogeneous one. Probabilities less than 1 per cent are significant statistically, and, in our case, suggest that there are differentials present other than those due to chance. Probabilities ranging from 5 to 1 per cent are borderline cases. In Table IV the data are tabulated by series for both larval and pupal duration.

The interpretation of the material of Table IV is not easy since the probabilities do not follow an exact pattern of differences. In general, however, the following points are suggested:

² A probability of 5 per cent signifies that there are 5 chances out of 100 of duplicating the observed results by random sampling.

1. The variability associated with pupal duration is less than that for the larval period. This is anticipated from the earlier studies. The analysis of variance shows that, when experiments are set up as these have been, there is rarely any great difference in the way pupae develop between one population and another. In other words, the experimental error involved in setting up a series of replicated populations is not great for this particular case.

2. The variance picture for larval duration is more erratic than for pupal duration. For example, in Series α , β , A and E there are two distinct sources of variability: between populations and within populations. In short, it does make a difference, in respect of rate of development, whether the larvae are cultured in one vial or in another. Contrariwise, Series B, C and D are homogeneous. The cause for these differences is not apparent.

The variance analysis of the material presented in this paper suggests that the technique has application for the population biologist. It is obvious that this statistical treatment of the data has not added anything specific about the biological factors at work in the populations. However, it has shown that such factors exist. The discrepancies in the data brought out by the analysis are not necessarily technical weaknesses. The variance material has not altered in any way the basic interpretations about inter-series (density) differences. It has been shown that, for some cases, there may be significant intra-series differences. It is probable that these are more complex for most populations since the total variability of the present experiments is small (the C.V.'s ranging from 4.5 to 15.5 per cent), and since the experiments have been run under carefully controlled conditions.

CONCLUSIONS

The specific points brought out in this paper are clear. By increasing the density of imaginal *Tribolium* the rate of development of the larvae can be retarded without affecting consistently the pupal stage. Furthermore, the evidence indicates that the duration of the larval stage is longer in crowded cultures because the flour is conditioned more rapidly there than it is in populations of low density. From the viewpoint of the population life-history these facts are important. To date it has been shown that unmolested cultures of *Tribolium confusum* decline with age primarily because they condition their environment through their own activity. This is a density effect since the rate of conditioning and the size of the population stand in direct proportion. However, it is not a behavior effect in the sense of direct inter-beetle competition.

Earlier investigations (Park and Woolcott, '37) have shown that conditioned flour lowers the fecundity of the beetles. Patently, this is correlated with population decline since fewer eggs are produced as the flour gets more conditioned. The recent study (Park, '38) on post-embryonic development showed that as the flour got more conditioned the larval mortality and length of the larval period increased. This held for flour conditioned by the larvae themselves. The present report adds to this knowledge by

showing that the same type of effect obtains if the imagoes, in contrast to the larvae, are responsible for the conditioning. These two studies taken together furnish another link to the investigation of the decline of *Tribolium* populations by showing that metamorphosis, as well as productivity, is an important factor in accounting for such decline. It is obvious that a population in which the larvae are not metamorphosing efficiently will be at a disadvantage when compared with one where such is not the case. The whole group of post-embryonic effects attain more significance and generality when it can be shown that they are induced by both larval and imaginal densities.

SUMMARY

When a series of *Tribolium confusum* populations are established consisting of a constant number of larvae (10) but a geometrically increasing number of imagoes (1, 4, 16, 32, 64) the following effects are noted:

1. The duration of the larval period is extended as the density of the imagoes increases.
2. The larvae living in crowded imago cultures grow more slowly in terms of body weight than those in less crowded cultures.
3. The duration of the pupal period is not significantly affected by the crowding of larvae with imagoes.

These facts are related to the ecology of populations and shown to have significance in contributing to the explanation of the decline of *Tribolium* cultures.

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INCREASE OF *SPOROBOLUS CRYPTANDRUS* IN PASTURES OF EASTERN NEBRASKA ¹

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The severe drought of 1934 to 1938 has resulted in great losses in the plant populations of native pastures. In Nebraska, little bluestem, *Andropogon scoparius*, and Kentucky bluegrass, *Poa pratensis*, have almost disappeared, while big bluestem, *Andropogon furcatus*, and numerous other important pasture grasses have suffered heavy losses. In addition to shiftings within the plant populations to compensate these losses, such as an enormous increase in side-oats grama, *Bouteloua curtipendula*, notable and widely spread local extensions have occurred. Over thousands of pastures western wheat grass, *Agropyron smithii*, has spread widely, and in similar numbers sand dropseed, *Sporobolus cryptandrus*, has become a dominant or the dominant species in these grazed areas.

Degeneration of prairies under the impact of grazing and subsequent changes in the vegetation under continuous pasturing have been consistently studied over a period of ten years. Examination of extensive field notes taken before the dry period began in 1932 reveals the fact that formerly the sand dropseed occurred only rarely or very sparingly. Following the destructive drought of 1934, it rapidly increased in abundance and in two or three years became one of the most important pasture grasses. Many inquiries have been received from farmers and stockmen regarding this "new pasture grass."

DISTRIBUTION

Sporobolus cryptandrus (Torr.) A. Gray is very widely distributed especially in light sandy soils almost throughout the United States. Although abundant westward, it is not common to true prairie (Weaver and Fitzpatrick, '34). Over the broad ecotone where true prairie gradually changes into mixed prairie the best limit of the former is set by the disappearance of *Stipa spartea* and *Sporobolus asper* which are replaced in the mixed prairie by *Stipa comata* and *Sporobolus cryptandrus* (Weaver and Clements, '38). Sand dropseed is common in all of the western range states, with the exception of California, but is most important in the Great Plains, the Southwest, and in portions of the drainage basins of the Clearwater, Salmon, and Snake Rivers in Idaho and Oregon (Range Plant Handbook, '37).

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CHARACTER ABOVE GROUND

This grass is a tufted perennial of xeric habit. In general the tufts are small but the larger bunches may have a basal diameter of 5 or 6 inches and 30 to 50 leafy stems, which form an open crown (fig. 1). The pithy, solid stems are mostly erect but some usually spread outward at various angles or may even grow parallel to the soil surface. Even vertical stems often spread outward at the base. The leaves are usually 5 to 12 inches long. They are



FIG. 1. A fine plant of *Sporobolus cryptandrus* about 3 feet tall. Note the basal spreading of the stems and the openness of the bunch.

flat, 2 to 5 mm. wide, with conspicuous, long, white tufts of hairs where the blade joins the sheath. Nearly all are confined to the lower half of the mature plant.

Growth in Nebraska is renewed in spring long after that of bluegrass, needle grass, *Stipa spartea*, June grass, *Koeleria cristata*, and other species of northern extraction, but earlier than that of the bluestems. By the middle of April the new leaves are an inch or more in length and enough new shoots occur at the bases of the old stems so that stock are tempted to graze the

bunches. This is discouraged, however, by the dried stem bases of the preceding year which stand stiffly often at an angle of 45° with the soil (fig. 2).

Growth is fairly rapid and if the plants are ungrazed a height of six or more inches is attained by the middle of June (fig. 3). Production of flower stalks begins about June 15, and during favorable seasons they are borne in great profusion and attain a height of 3 feet. But during dry years they may be reduced to one-third the normal size. The pale or leaden to purplish panicles are partly enclosed in the topmost leaf sheathes. The unenclosed portion spreads somewhat but the panicle is usually narrow. The larger ones are often 15 inches long. Blossoming begins late in June and may continue until October.



FIG. 2. A thin stand of sand dropseed in a heavily grazed pasture showing the new growth of leaves on April 24, 1938.

The seeds, which mature in late summer or early fall, are produced in enormous numbers. Ten thousand mature seeds have been obtained from a single enclosed panicle. Their total weight was only 0.7 gram. Germination as high as 80 per cent has been obtained but more usually only 25 to 30 per cent. The small seeds gradually fall out of the enclosing leaf sheath and may readily be carried along the ground by high winds to considerable distances. They frequently lie dormant for many years. A germination of 74 per cent after twenty years has been obtained in some experiments where the seeds were buried in pots 3.5 feet below the soil surface (Goss, '24). Seedlings develop rapidly. Tillers appear only a few weeks after germination

and soon the seedling becomes a small tuft or bunch of leafy stems. Plants with 5 or 6 tillers and 10 to 12 roots were observed the first week in July. Thereafter the growth of ungrazed plants is even more rapid. Several flower stalks are produced and seeds ripen, thus completing the round of life in a single year. When this dropseed is protected or properly grazed it tends to increase in depleted pastures.

When drought comes the leaves roll tightly, the osmotic pressure rising from 10 or 12 to 35 or 40 atmospheres. But soon they unroll and resume photosynthetic activity even after relatively light showers. This is due to the excellent provision for absorption in the surface soil.

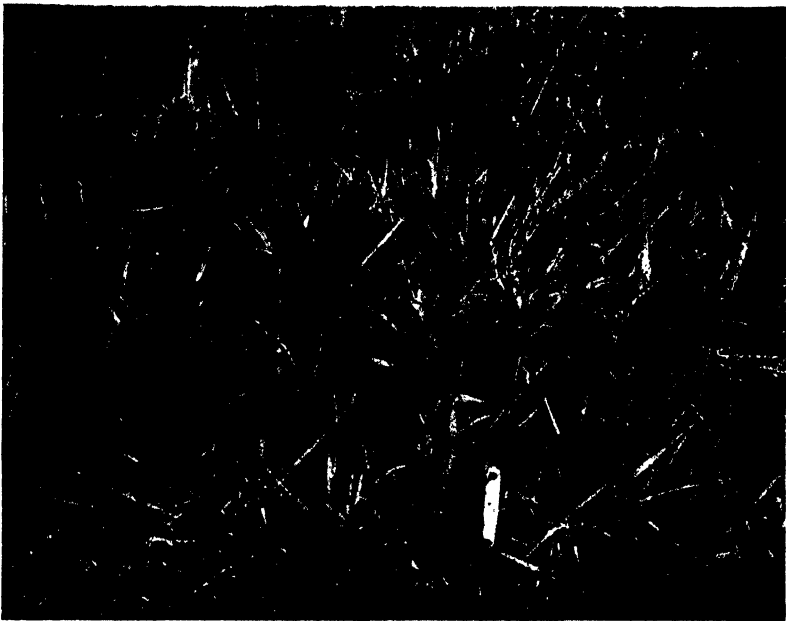


FIG. 3. Detail of *Sporobolus cryptandrus* in a former bluegrass pasture on June 15, 1938. The plants, which have not yet been grazed, are 6 inches tall.

THE ROOT SYSTEM

The mature root system was studied during the dry summer of 1937 and the more favorable one of 1938. In the earlier study the subsoil had been very dry for several years and prevented deeper root penetration. The greatest root depth attained was 22 inches and a maximum lateral spread from the base of the plant was 9 inches. Of the thirteen plants examined, the average number of roots per stem was 4.3. At the second examination soil moisture had penetrated to approximately 4 feet and the longest roots were found growing vigorously to this depth. Even the main roots are only a millimeter or two in diameter and the branches are very fine. As many as

40 laterals per linear inch are not uncommon. Some of these laterals are several inches in length and densely clothed with fine rootlets of the third and fourth order.

Few roots penetrate directly downward. Nearly all extend outward 4 to 8 inches at various angles to about 45° with the surface before turning downward. Usually they then pursue a directly downward course. Many extend horizontally throughout their entire length (3–11 in.) in the surface two inches of soil. This portion of the root system is perhaps most freely branched and fine rootlets spread everywhere to within a radius of approximately a foot about the plant. Beneath, the well branched, deeper roots afford an excellent absorbing system. Average number of roots per stem was 3.5, one large plant with 46 stems possessing more than 150 main roots. Thus, the mature root system consists of a vast network of small roots and masses of finely branched rootlets. The soil beneath the plant and several inches on all sides is filled with a dense mat of roots to a depth of about 4 feet. Such an absorbing system is remarkably efficient.

It is believed that with additional depth of moist soil this species would penetrate even deeper under the impact of continued drought. Such has been found to be the case with *Stipa spartea* where the roots were traced in moist mellow soil to a depth of slightly over 8 feet. This depth, determined in 1938, exceeded any previous depth-record by about 3 feet.

PALATABILITY, FORAGE PRODUCTION, AND BEHAVIOR UNDER GRAZING

Throughout the west, sand dropseed produces a fairly large amount of foliage which is eaten by all classes of livestock. Its palatability, of course, varies greatly, depending upon the climatic conditions under which it grows. Hence the rating is from fair to very good. In eastern Nebraska, both cattle and horses graze it readily, often in preference to western wheat grass. Not only are the leaves eaten but also the stems and flower stalks at all stages of development. The plants are often grazed closely even where forage is abundant. Many stockmen of eastern Nebraska consider it a good forage species.

Total production under constant grazing was determined during 1938. Five clippings were made in the pasture where the growth during the three-weeks interval between clippings was protected by a series of small portable exclosures. The grass in the 30-square-foot area in each pasture exclosure was clipped at the soil surface and from the dry weight produced was subtracted the dry weight of the uneaten remnants of dropseed from adjacent areas of similar size. Thus, the approximate amount eaten by the stock was obtained. Neither lot of clipped areas was used for a second cutting, the exclosures being constantly relocated. The forage removed from the pasture by the cattle was 2.02 tons per acre.

Owing to the semi-prostrate nature of some leafy stems, grazing does not injure this grass as much as it does many more erect mid grasses (fig. 4). The vigor of this species and its ability to reseed, even under rather heavy stocking, because of prostrate or semi-prostrate flower stalks, adds to its value as a pasture plant. It withstands close grazing far better than *Stipa spartea*, *Sporobolus heterolepis*, or even *Andropogon scoparius*. When protected or properly grazed it tends to increase in depleted pastures. Thus, many of the former bluegrass and little-bluestem pastures of eastern Nebraska are now populated with a good cover of sand dropseed. On the other hand, some



FIG. 4. Well grazed plants of the sand dropseed showing the manner in which prostrate and often more erect flower stalks are left unharmed. These furnish abundant seed for reproduction.

pastures have been so greatly abused during the drought period that the once fine stand of dropseed is now represented only by dead crowns and a few, small, weak survivors of this once abundant grass.

RELATION TO EROSION

An important function of range and pasture grasses is that of protecting the soil against wastage by erosion. Studies on the amounts of underground plant materials in various types of pastures as well as their resistance to water erosion under similar conditions of slope, etc., have been made, including some work on sand dropseed (Weaver and Harmon, '35; Kramer and Weaver, '36). The thorough manner in which the roots of this species in a good stand

occupy the soil is shown in figure 5. Dry weight of this material (about 140 grams per one-half square meter) in the first four inches is 1.5 tons per acre, which is somewhat less than that of little bluestem or bluegrass under pre-drought conditions. The trampled pasture soil is held almost as firmly, however, and for as long a period of time against water erosion as that occupied by wheat grass or bluegrass.

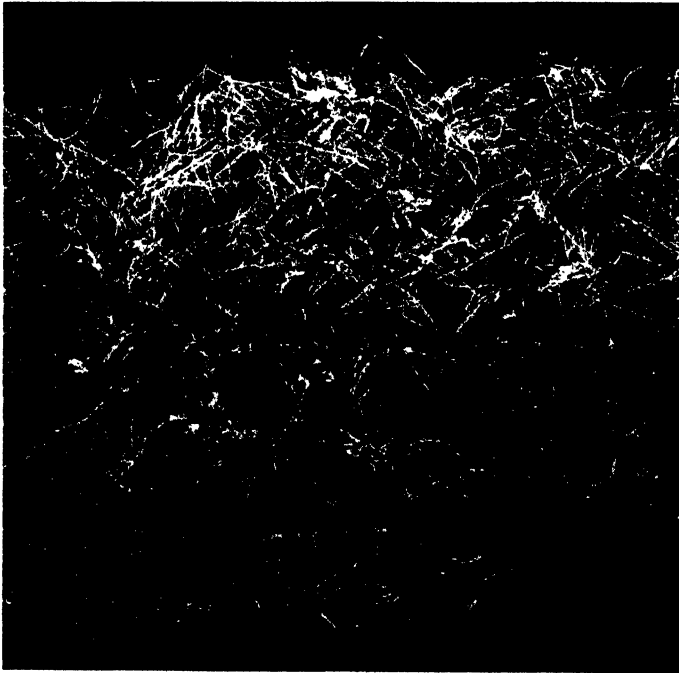


FIG. 5. Roots from a block of sod 4 inches deep and 50 × 50 inches in area showing the great underground network of the sand dropseed.

SUMMARY

Sand dropseed, *Sporobolus cryptandrus*, occurred only rarely and sparingly in native pastures of eastern Nebraska before the great drought of 1934. It has since increased so rapidly that it is now one of the most abundant and important pasture grasses. This species, of wide distribution westward, "renews growth in early spring, develops rapidly, and is not readily injured by close grazing. It is a prolific seeder and under proper grazing soon reclaims pastures where bluegrass and little bluestem have died. Its resistance to drought is due in part to an excellent root system. In eastern Nebraska, it is of good palatability, produces much forage, and is efficient in protecting the soil against loss by erosion.

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AN ECOLOGICAL STUDY OF THE MAMMALS OF THE BADLANDS AND THE BLACK HILLS OF SOUTH DAKOTA AND WYOMING

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The survey upon which this report is based was made to determine the ecological distribution of the mammals of the Badlands and of the Black Hills of western South Dakota and adjacent parts of Wyoming; and to attempt to ascertain some of the factors influencing mammalian distribution in these regions.

The original data were gathered in the field by the author during the summer of 1934. The period from June 23 to August 4 was spent in making a study of a section of the eastern portion of the Badlands, and the period from August 7 to August 25 was spent similarly in the south-central portion of the Black Hills.

The specimens of mammals collected are deposited in the Museum of Zoology at the University of Michigan. The live *Peromyscus* were sent to the Laboratory of Vertebrate Genetics at the same institution.

The technical names for the mammals follow Miller ('23), except where changes were made subsequently. The use of *Mephitis mephitis hudsonica* follows Hall ('36, p. 64) and that of *Citellus tridecemlineatus pallidus* for the striped ground squirrel of the Black Hills follows Howell ('38, p. 113). The common names are taken mostly from Anthony ('28). The names for the plants follow Rydberg ('22).

I feel especially grateful to F. M. Gaige and to L. R. Dice of the Museum of Zoology at the University of Michigan for making the necessary funds available to undertake this project, and for the unselfish help they have given in other ways. To the late A. G. Granger, formerly of Kadoka, South Dakota, I am indebted for the unlimited hospitality he extended while I was at his ranch in the Badlands. Thanks are due further to the officials of the game and fish commissions of South Dakota and Wyoming for granting permission to collect mammals in their respective states. W. H. Burt kindly checked my identifications of the mammals.

PHYSIOGRAPHY

The physiography of the two regions under consideration is vastly different. The Badlands, lying in southwestern South Dakota within the southern portion of the unglaciated Missouri Plateau, form an amphitheater

intricately adorned through the action of erosive forces (Fig. 1). Essentially, they extend in a southwest-northeast direction and cover an area of approximately 3,700 square miles. They occur (Fenneman, '31, p. 67) where the old gently undulating peneplain is being actively dissected by renewed erosion. The elevation varies from 2,000 feet to some 2,500 feet above sea-level. The White River, which courses through the central part of the region, forms the principal drainage channel. Its tributaries are mainly responsible for the erosion now in progress. In the northwestern section of the region, the southeasterly branches of the Cheyenne River supplement the work of the White River system. Within the region there are several extensive "tables," remnants of the original peneplain, which rise to elevations of 500 to 600 feet above the basin of the White River (Fenneman, '31, p. 67).



FIG. 1. A general view of the Badlands from Kodak Point, Washabaugh County.

The northern boundary of the Badlands is known locally as the "Wall" (Fig. 2) which it is indeed. It extends precipitously as an unbroken rampart from the vicinity of Kadoka on the east to Wasta on the west. Similar walls or bluffs are developed throughout the Badlands on the sides of stream basins. Forming the conspicuous physiographic division between the uplands and the lowlands, the bluffs are a prominent feature, for it is upon them that the badland topography is developed. The boundary of the Badlands on the south is roughly co-extant with the Pine Ridge, which is topographically similar to the Wall.

The White River formation, from which the Badlands are sculptured, consists of extremely pale colored and fine, poorly consolidated pure and sandy clays (Fenneman, '31, p. 69); and interbedded among the several strata comprising the formation are scattered horizons of concretions, gravels, and lenses of sandstone. The sandstone beds, being relatively more resistant to erosion, are responsible for the local terracing and castellation.



FIG. 2. A portion of the Wall near Cedar Pass, Jackson County; shows a portion of the denuded and the yellow pine-red cedar woodland associations.

The Black Hills (Fig. 3), which lie in western South Dakota and northeastern Wyoming, are separated from the Badlands by a strip of the Great Plains varying in width from fifteen to twenty miles. They are an isolated mountain mass resulting from an igneous domal uplift, and although much reduced as a result of subsequent erosion, they still reach an altitude of 7,216 feet above sea-level. Extending in a southeast-northwest direction, they cover an area of approximately 7,200 square miles, and are entirely surrounded by the Missouri Plateau section of the Great Plains (Fenneman, '31, p. 61). On the east, they rise above the plains about 4,000 feet and on the west about 3,000 feet.



FIG. 3. A portion of the French Creek Valley $3\frac{1}{2}$ miles east of Custer. Pine forest in the background.

CLIMATE

There is considerable diversity between the climate of the Badlands and that of the Black Hills. The minimum temperatures average less, and the maximum temperatures greater in the Badlands than in the Black Hills. In the first region, the annual precipitation is much less, and the growing season longer than in the second.

VEGETATION AND SOILS

There are three vegetational types, namely: grasslands, stands of broad-leaved trees, and stands of coniferous trees, which are common to both the Badlands and the Black Hills. In the Badlands the grasslands are by far the most extensive type of ground cover. The broad-leaved trees usually occur as woodlands or groves, which are developed mainly in the drainage channels. Likewise, the stands of conifers usually occur as woodlands, but they are found chiefly on the bluffs of the Badlands. In the Black Hills the grasslands are found mostly on the slopes of the foothills, but even at the higher altitudes there are isolated areas of grasslands. As in the Badlands, the broad-leaved trees occur mainly in the drainage channels, but usually in denser stands. The conifers (mostly western yellow pine), however, occupy the upper slopes in a forest stand, which is the most extensive type of cover in the Black Hills.

While there is considerable diversity in the prevailing climates of these two regions, it is not believed that their variations account entirely for the differences that are apparent in the extent and the densities of these three vegetational types. The distribution of the soil types also seems to be important.

In situations characterized by very moist sandy to gravelly soils, stands of broad-leaved trees occur as the predominant vegetational type. This combination of soil moisture and texture is commonly found adjacent to water-courses. Cottonwoods and willows appear as the conspicuous vegetation in the Badlands where they develop a woodland or grove type of stand. In the Black Hills bur oak, quaking aspen, paper birch, and willow comprise the prominent vegetation, but they form a somewhat denser stand.

On the dry, unstable bluffs of the Badlands, vegetation is for the most part absent. The soils are mostly fine-textured and hard, baked clays. Where the slopes are more gentle and stable, localized stands of western yellow pine and western red cedar occur. The yellow pines appear to be confined to these xeric sites, but a few of the red cedars find their way to the floors of some of the basins, where they grow widely scattered. Were it not for the fact that the more precipitous bluffs are exposed more severely to erosive forces, it is likely that the pine and the cedar would have a more extensive distribution in the Badlands. In the Black Hills, too, the most extremely exposed sections are devoid of vegetation. The crown of Hearney Peak and

the Needles section are representative. Apparently no climatic timberline exists in this region, the timberline present probably being due instead to a lack of soil and extreme exposure to the erosive action of wind and rain. On the dry slopes which characterize the greater part of this region, however, a xeric coniferous forest composed principally of western yellow pine is developed. On the lower western slopes of the Black Hills the pines give way in some cases to western red cedars in the slightly more moist situations. Bedrock usually lies very close beneath the thin mantle of surface soil.

Where intermediate soil conditions prevail in either region, the grasses are most conspicuous. These soils vary somewhat in texture, but usually they are fine. Ordinarily they lie in deep beds on a horizontal or gently rolling plain. In the Badlands the soils are generally heavier in the grasslands than they are in the Black Hills, where the soils are loamier.

MAMMALIAN HABITATS OF THE BADLANDS REGION

Uplands.—The term "upland" as used here denotes that part of the unglaciated Missouri Plateau in which badland topography has not yet been developed, in contradistinction to the lowlands found within the badland basins, which consist of soils reworked from the uplands.

1. The buffalo-grama grass association: The portions of this habitat which were studied from June 23 to August 3 were located mainly south of Kadoka in Jackson County and south of the White River in Washabaugh County. The short grasses, namely: buffalo grass (*Bulbilis dactyloides*) and grama grass (*Bouteloua gracilis*) (Petty, '26, p. 550; Weaver & Clements, '31, p. 465), are the dominant plants of this association. Soapweed (*Yucca glauca*), prickly pear cactus (*Opuntia polycantha*), and several species of sage brush (*Artemisia spp.*) are conspicuous components. Much of this land has been put under cultivation for raising forage crops such as corn, Sudan grass, and millet for the purpose of supplementing the native forage available to livestock through the winter months. (The numerals following the names of the mammals in each of the habitat lists which follow indicate the number of specimens secured of that species in that particular habitat.) The following mammals were collected: Northern skunk (*Mephitis mephitis hudsonica*) [1]; Badger (*Taxidea taxus taxus*) [1]; Pale striped ground squirrel (*Citellus tridecemlineatus pallidus*) [4]; Black-tailed prairie dog (*Cynomys ludovicianus ludovicianus*) [6]; Kansas pocket mouse (*Perognathus hispidus paradoxus*) [1]; Osgood deer mouse (*Peromyscus maniculatus osgoodi*) [6]; White-tailed jack rabbit (*Lepus townsendii campestris*) [7]; Wyoming cotton-tail (*Sylvilagus audubonii baileyi*) [1].

2. The cottonwood-willow association: A brief study was made of this habitat on July 8 along Brady Creek about 5 miles northwest of Kadoka in Jackson County. It is confined to the borders of the stream courses on the uplands. Cottonwood (*Populus Sargentii*), willow (*Salix spp.*), hackberry

(*Celtis occidentalis*), and sage brush form the most conspicuous plants. Only a part of one day was spent in this habitat, but inasmuch as one species of mammal was found here that was taken nowhere else, it is believed that the recognition of this association is justified. The following mammals were collected: Nebraska cottontail (*Sylvilagus floridanus similis*) [4].

Bluffs. It is in this physiographic subdivision that the "badland" topography is developed. It includes the canyon-sides and the Wall which extends from the vicinity of Kadoka on the east to the vicinity of Wasta on the west. This physiographic type, which forms the transition locally between the uplands and the lowlands, has two recognizable divisions.

1. Denuded: The sections which were studied from July 10 to August 3 comprised the bluffs of Cottonwood Canyon in Washabaugh County, and the Wall in Jackson County from near Kadoka to Cedar Pass. As the term implies, these parts of the bluffs are nearly devoid of plant life. Being in a state of active erosion, it appears that no plants are able permanently to establish themselves. Occasionally a plant will take root, but usually not for long. As a result of one torrential shower, it may be destroyed and washed away. The following mammals were collected: Badland chipmunk (*Eutamias minimus cacodemus*) [21]; Osgood deer mouse (*Peromyscus maniculatus osgoodi*) [12]; Pale bushy-tailed woodrat (*Neotoma cinerea rupicola*) [7]; White-tailed jack rabbit (*Lepus townsendii campestris*) [2]; Wyoming cottontail (*Sylvilagus audubonii baileyi*) [2].

2. Yellow pine-red cedar association: Occasionally, where slumping has occurred, shelves of varying dimensions have been formed along the bluffs. Because their surfaces are usually fairly level and stable, they have either retained or have become covered with a sod of grasses or a stand of trees and shrubs or both. The woody forms include in order of relative prominence, western red cedar (*Sabina scopulorum*), western yellow pine (*Pinus scopulorum*), rabbit brush (*Chrysothamnus spp.*), and sage brush. In small localized depressions wolfberry (*Symphoricarpos occidentalis*), currant (*Ribes inebrians*), and rose bushes (*Rosa arkansana*) form dense thickets ranging in height from one to three feet. This habitat was studied principally at Cedar Pass (30 miles west of Kadoka) from July 31 to August 3. The following mammals were collected: Osgood deer mouse (*Peromyscus maniculatus osgoodi*) [3]; Hayden vole (*Microtus haydenii*) [1]; Nebraska yellow-haired porcupine (*Erethizon epixanthum bruneri*) [Yellow pines, which were apparently "barked" by porcupines, were observed on the bluffs of Cottonwood Canyon]; Wyoming cottontail (*Sylvilagus audubonii baileyi*) [3].

Lowlands. These are essentially imperfectly leveled floors of basins which have been carved out of the uplands. While shallow box canyons may sometimes be developed upon them, they generally vary but slightly in contour. Some of them are fairly extensive and may cover areas up to 25 square miles or more. Many stream beds wind their way tortuously over the low-

lands, but by far the greater number of them are dry except when carrying run-off waters. Two associations occur in this physiographic subdivision.

1. Buffalo-grama grass association: As on the uplands, these short grasses are again the predominating vegetation. Relatively extensive patches of prickly pear cactuses occasionally develop, likely as a result of overgrazing by domestic livestock. Sagebrush and soapweed are present in a rather scattered and unthrifty state of development. This association was studied principally on the floor of Cottonwood Basin in Washabaugh County from June 23 to July 24. The following mammals were collected: Northern skunk (*Mephitis mephitis hudsonica*) [4]; Badger (*Taxidea taxus taxus*) [1]; Prairie coyote (*Canis lestes nebrascensis*) [2]; Pale striped ground squirrel (*Citellus tridecemlineatus pallidus*) [1]; Black-tailed prairie dog (*Cynomys ludovicianus ludovicianus*) [5]; Osgood deer mouse (*Peromyscus maniculatus osgoodi*) [29]; White-tailed jack rabbit (*Lepus townsendii campanius*) [5]; Wyoming cottontail (*Sylvilagus audubonii baileyi*) [1].

2. Cottonwood-willow association: This habitat was studied chiefly on the floodplain of the White River and Cottonwood Creek from June 23 to July 24. The latter is a southerly tributary stream in Washabaugh County. Cottonwoods and willows form the most prominent floral elements, but elm (*Ulmus americana*) and boxelder (*Negundo nuttallii*) are not uncommon. Occasionally, a buffalo berry (*Lepargyrea argentea*) occurs. This growth forms a rather luxurious grove-like stand on the floodplain of the White River. Along the tributary streams, however, it is considerably less dense. Scattered red cedars invade the upper reaches of these latter situations. The thin stands on the basin floors indicate that the soil in these situations is drier than it is on the White River floodplain. The following mammals were collected: Northern skunk (*Mephitis mephitis hudsonica*) [1]; Say bat (*Myotis subulatus subulatus*) [2]; Pale brown bat (*Eptesicus fuscus pallidus*) [1]; Eastern raccoon (*Procyon lotor lotor*) [1]; Western fox squirrel (*Sciurus niger rufiventer*) [3]; Maximillian pocket mouse (*Perognathus fasciatus fasciatus*) [1]; Kansas pocket mouse (*Perognathus hispidus paradoxus*) [2]; Missouri River beaver (*Castor canadensis missouriensis*) [1]; Prairie harvest mouse (*Reithrodontomys megalotis dychei*) [6]; Osgood deer mouse (*Peromyscus maniculatus osgoodi*) [5]; House mouse (*Mus musculus musculus*) [1].

MAMMALIAN HABITATS OF THE BLACK HILLS REGION

1. Western yellow pine association: This association forms a forest composed dominantly of western yellow pine, which appears to be extremely tolerant to xerophytic conditions. It occupies upland sites where the soil is coarse and well drained and in the summer quite warm. Altitudinally, it ranges from about 3,500 feet above sea-level on the east and 4,000 feet on the west to an elevation of about 6,000 or 7,000 feet. At the higher levels, the yellow pine develops beautiful park-like forests; whereas on the lower

sites, the trees form an open woodland. Western red cedars (especially in the western section), wild rose (*Rosa acicularis*), bunch grasses, and prickly pear cactus are prominent associates. Studies were made of this habitat in the vicinity of Otis, Custer County, South Dakota, and east of Newcastle, Weston County, Wyoming, from August 7 to 24 inclusive. The following mammals were collected: Black Hills marmot (*Marmota flaviventris dakota*) [A colony of these mammals was observed at an outcrop of granite near Doran's ranch about three miles east of Custer. It was located almost at the contact between the yellow pine forest and the mountain prairie]; Northern chipmunk (*Eutamias minimus borealis*) [3]; Black Hills chickaree (*Sciurus hudsonicus dakotensis*) [4]; Osgood deer mouse (*Peromyscus maniculatus osgoodi*) [23]; Badlands white-footed mouse (*Peromyscus leucopus aridulus*) [2]; Colorado bushy-tailed woodrat (*Neotoma cinerea orolestes*) [1]; Short-tailed red-backed vole (*Clethrionomys brevicaudus*) [1]; Nebraska yellow-haired porcupine (*Erethizon epixanthum bruneri*) [2]; American wapiti (*Cervus canadensis canadensis*) [Observed]; Mule deer (*Odocoileus hemionus hemionus*) [Common].

2. Bur oak association: Along the borders of the streams in the Black Hills, the pines give away to deciduous trees. The streams are usually located in canyons, and the fluvial soils are cool, moist, and somewhat more finely textured than the pine-clad uplands. The most prominent species of trees are: bur oak (*Quercus macrocarpa*), quaking aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*). Studies of this habitat were made from August 7 to 25 mainly along Grace Coolidge Creek (formerly Squaw Creek) in Custer State Park. The following mammals were collected: Little long-eared bat (*Myotis evotis*) [3]; Mountain bobcat (*Lynx uinta*) [1]; Northern chipmunk (*Eutamias minimus borealis*) [17]; Black Hills chickaree (*Sciurus hudsonicus dakotensis*) [3]; Osgood deer mouse (*Peromyscus maniculatus osgoodi*) [6]; Badlands white-footed mouse (*Peromyscus leucopus aridulus*) [1]; Mule deer (*Odocoileus hemionus hemionus*) [Common].

3. Mountain prairie association: In certain situations in the Black Hills where the soil texture, moisture, and depth appear to reach a favorable balance, a grassland or prairie type of habitat is developed. The particular one studied, which was located in the vicinity of Doran's ranch about three miles east of Custer, appears to be a natural prairie, for no evidence indicating the presence of a former forest was discovered. And in a photograph taken by Illingworth in 1874 (O'Hara and Connolly, '26, pl. 9) it appears to be much the same as it did when this survey was made from August 13 to 17, 1934. (Illingworth was the official photographer with General G. A. Custer's Black Hills expedition in the summer of 1874.) In 1934 a dam was built across French Creek near here, and by the summer of 1936 much of this prairie was inundated. The elevation of this prairie ranged from 5,200 to 5,500 feet above sea-level, and in places it approached a width of 2 miles.

The most prominent plants were the short grasses, but clumps of sage brush (*Artemisia spp.*), golden rod (*Solidago sp.*), butter and eggs (*Linaria Linaria*), and asters (*Aster sp.*) were conspicuous. The following mammals were collected: Pale striped ground squirrel (*Citellus tridecemlineatus pallidus*) [2]; Northern chipmunk (*Eutamias minimus borealis*) [1]; Black Hills pocket gopher (*Thomomys talpoides nebulosus*) [4]; Osgood deer mouse (*Peromyscus maniculatus osgoodi*) [7]; Black Hills cottontail (*Sylvilagus nuttallii grangeri*) [1].

4. Riparian association: This association, which was studied from August 13-17 along a portion of French Creek and a small creek that flowed into it in the vicinity of Doran's ranch, is restricted to the streams and their banks. Before the area was flooded, sedges (*Carex spp.*), rushes (*Juncus sp.*), and flags (*Iris missouriensis*) were prominent plants along the banks. The following mammals were collected: Black Hills marmot (*Marmota flaviventris dakota*) [1]; Osgood deer mouse (*Peromyscus maniculatus osgoodi*) [1]; Sawatch meadow vole (*Microtus pennsylvanicus modestes*) [3]; Great Plains muskrat (*Ondatra zibethica cinnamomina*) [1].

DISCUSSION

Distribution of the Mammals. While it is frankly admitted that the time spent in the field was of too short duration to study thoroughly either region or to make a complete collection of all the mammals, nevertheless it seems that a few remarks concerning mammalian distribution are justified.

Fourteen (64 per cent) of the 22 species and subspecies of mammals found in the Badlands are characteristic of the Great Plains generally. Two races, namely, *Eutamias m. cacodemus* and *Neotoma c. rupicola* are peculiar to the badland regions in the northern Great Plains. The range of the chipmunk, however, is less extensive than that of the woodrat.

The mammals of the Black Hills represent mostly a mixture of Great Plains and Rocky Mountain forms. Three species and subspecies, namely, *Sciurus h. dakotensis*, *Thomomys t. nebulosis*, and *Clethrionomys breviceaudus* are peculiar to this region.

Of the 37 species and subspecies collected, only two species, *Eutamias minimus* and *Neotoma cinerea*, and four subspecies, *Citellus t. pallidus*, *Peromyscus m. osgoodi*, *Castor c. missouriensis*, and *Erethizon e. bruneri*, are, so far as known, common to both regions. There may be other forms which are common to both regions, but it is very probable that definite habitat preferences or tolerances prevent most of the mammals from being equally at home both in the Badlands and in the mountains.

Two species which occur both in the Badlands and in the Black Hills are represented by distinct races in each of the regions. *Eutamias minimus* is represented in the former region by the subspecies *cacodemus*, and in the latter by *borealis*. Similarly, *Neotoma cinerea* is represented in the former region

by the subspecies *rupicola*, and in the latter by *orolestes*. In both species, the geographic ranges of the Badlands races, so far as they are known, are less extensive than the ranges of their Black Hills counterparts. This seems to be particularly true of *Eutamias m. cacodemus*. Furthermore, the local distribution of each species in the Badlands appears to be restricted to the bluffs, for intensive trapping adjacent to them, both above and below, resulted in no captures.

Soil and Pelage Colors. The Badlands races of both the chipmunk and the woodrat are strikingly pale in pelage color, whereas the Black Hills races are definitely darker. The soils of the habitat of the Badlands races are predominantly a pale grayish white in hue. The monotony of this tone is broken occasionally by horizontal bands of rust or grayish green in pastel shades. The chipmunk and the woodrat are both conspicuously of a pallid whitish gray hue, which becomes somewhat darker on the dorsal surface and a pure white on the ventral surface. In addition, the dorsal stripes of the chipmunk are weak shades of cinnamon and smoky gray.

The soils of the habitat of the Black Hills races are dark in color, varying from reddish brown to blackish. The chipmunk here is mostly a rich chestnut brown in color. On the ventral surface, however, the pelage becomes a smoky gray color. The woodrat of the Black Hills is definitely darker than the Badlands race, but the two races do not contrast nearly as sharply as do the two subspecies of chipmunks.

The Osgood deer mouse also shows a tendency toward a certain degree of correlation between the color of its pelage and the hue of the soil upon which it occurs. The Black Hills representatives tend to be dark in color, while those in the Badlands vary from dark to very pale buff colored individuals. There seems to be a further tendency for the pallid individuals to be somewhat restricted to exposures of pale colored soils. It is possible that the Badlands are in an area of intergradation between this form and the bright buffy *Peromyscus m. nebrascensis* of the sandhills of northwestern Nebraska, which lie to the south of the Badlands. It seems unlikely, however, that intergradation alone accounts for the occurrence of the pale-colored deer mice on the pale-colored soils of the Badlands.

A physical factor of the environment with which this variation in pelage color can be readily correlated is the color of the soil upon which these mammals live. This relationship has already been pointed out by many authors, but the most complete statement of it up to this time is given by Dice and Blossom ('37, pp. 107-108) when they declare, "A general statement of the rule governing mammalian pelage color is: The dorsal pelage colors of terrestrial mammals tend to match the color of the soil of their respective habitats."

The correlation between pelage color and soil color, moreover, seems to be most close in those habitats where the soil is exposed extensively through the lack of a heavy cover of vegetation. Both the chipmunk and the woodrat of

the Badlands are confined in their distribution to the bluffs, which are for the most part devoid of a cover of vegetation. They are living, therefore, on an extensive area of exposed soil. In their study, Dice and Blossom ('37, pp. 76-92) have listed a number of species showing geographic color variations in the region upon which their study is based. Among the many examples illustrating the correlation between pelage and soil color they describe, the most conspicuous are those of *Perognathus apache gypsi* (p. 79), which is a strikingly whitish colored pocket mouse from the White Sands of New Mexico; and *Perognathus intermedius ater* (p. 81) and *Neotoma albigula melas* (p. 90), which are respectively a very dark to blackish colored pocket mouse and woodrat from the black Tularosa Malpais of New Mexico. Blossom ('37, p. 3) further reports that three genera of mammals, namely, *Eutamias*, *Perognathus*, and *Ochotona* "have developed dark-colored races on the dark lavas of the Craters of the Moon."

On the bluffs of the Badlands with their extensive exposures of grayish white soils, two forms occur, a chipmunk and a woodrat, whose whitish gray pelts blend remarkably in hue with that of the soils upon which they are living. In the Black Hills, where the soils are for the most part covered with a mantle of vegetation, but where they are dark reddish brown to blackish in color, there is a corresponding correlation between the soil colors and the pelage colors of the Black Hills counterparts of the Badlands forms. Thus there appears to be a tendency for the pelage colors of mammals to correlate directly with the prevailing shades of color of the soils upon which they live. This correlation, furthermore, seems to be most distinct where soils are mainly or entirely lacking in a cover of vegetation.

SUMMARY

The mammalian habitats of each region studied are identified. These are for the Badlands: the upland buffalo-grama grass association, the upland cottonwood-willow association, the denuded bluffs, the bluff yellow pine-red cedar association; the lowland buffalo-grama grass association, and the lowland cottonwood-willow association. For the Black Hills are the following associations: the western yellow pine, the bur oak, the mountain prairie, and the riparian.

Of the 37 species and subspecies of mammals collected, only two species are, so far as known, common to both regions. The strongest manifestation of habitat preference is shown by two subspecies, both of which appear to occur only on the bluffs of the Badlands.

The Badland's races of both *Eutamias minimus* and *Neotoma cinerea* are strikingly pallid in pelage color, whereas the Black Hills races are decidedly brighter and darker. The pelage hues, furthermore, correlate closely with the general color tone of the soils upon which these forms live. *Peromyscus m. osgoodi*, too, shows a tendency toward this correlation.

The correlation between the general color tone of the pelage and that of the soil seems most close in those habitats where the soil is exposed extensively through a lack of a heavy cover of vegetation.

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FLUCTUATIONS IN THE ANNUAL VEGETATION OF CALIFORNIA

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The herbaceous vegetation of some 25,000,000 acres of California range lands is dominated by annual plants. This carpet of vegetation is often referred to as the "annual type." It constitutes the vegetation of extensive valley and foothill grassland areas and forms the ground cover under the more open woodland and chaparral types.

Under the influence of such factors as arid climate and variable weather, of livestock grazing and other treatment, this annual-plant cover undergoes changes that are both swift and erratic in comparison with the more stable perennial plant associations. Wide variations often occur from year to year in composition and volume. Moreover, such variations are the rule, not the exception. These fluctuations have long been recognized; but comparatively few attempts have been made to measure them. Since 1934, data on their occurrence and magnitude have been obtained in connection with the general program of range investigations at this station, since they bear directly on livestock production and watershed management. Illustrative examples are discussed in this paper. Supporting data were gathered on (1) the San Joaquin Experimental Range, an area of 4,500 acres in the woodland type in the foothills of Madera County; (2) a 40-acre outpost of the Experimental Range, also in the woodland type; and (3) a range reconnaissance of approximately 9,500,000 acres of the San Joaquin Valley, based on 2,570 sample plots distributed in 14 counties.

EXTENT AND CHARACTER OF CALIFORNIA'S ANNUAL-PLANT COMMUNITIES

The annual types cover most of the untilled plains and foothills of the Sacramento and San Joaquin Valleys, a large portion of the south Coast Ranges and part of the north Coast Ranges, as generalized in figure 1. They lie chiefly in the Lower and Upper Sonoran life zones. Areas in the Mohave Desert and in the Great Basin extension into eastern and northeastern California are not shown or included in this discussion, for they represent a somewhat different condition.

The climate prevailing in the annual-type area is characterized by the prevalence of wet winters and dry summers. The precipitation, largely in

¹ Maintained by the United States Department of Agriculture at Berkeley, California, in cooperation with the University of California.

the form of rain, usually begins in October or November and ends in April or May. Rainfall is thus distinctly seasonal. About two-thirds of the rain falls in the four months from December through March. Very light showers may occur from May to September. The yearly precipitation ranges from less than 10 inches up to 40, and varies widely from place to place and from

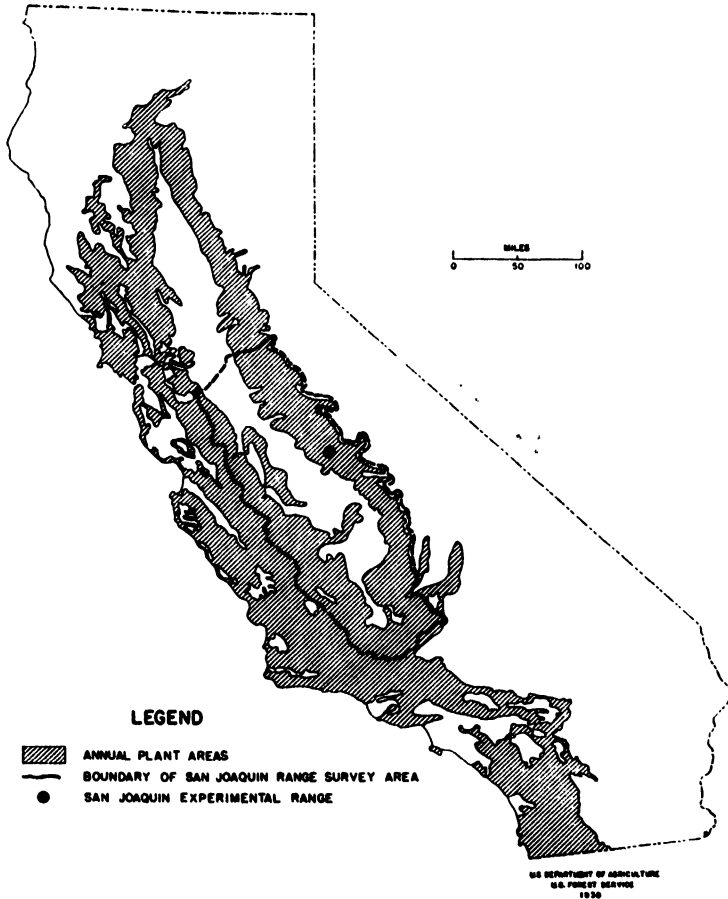


FIG. 1. California range areas in which annuals are generally dominant in the herbaceous cover. Included in this generalized territory are local saltgrass areas dominated by perennials, also dense woodland and chaparral areas in which annuals are negligible.

season to season. Winter temperatures may fall slightly below freezing for short periods. Summer temperatures in the Great Valley are relatively high, often exceeding 105° F. for several days in succession. Along the coastal areas the temperatures are more moderate. The relative humidity during the dry season is generally low, except near the coast. High wind velocities are rare.

By a very general classification, the annual-type area may be subdivided into three broad types of vegetation: treeless "grassland," woodland, and chaparral.² Grassland areas occupy the heart of the Sacramento and San Joaquin Valleys and much of the Coast Ranges. Bordering the grassland, and chiefly above it (fig. 2), lies the woodland zone which intermingles with and grades into chaparral. In turn the chaparral merges into the conifer belt above it.

The preponderance of annuals in the ground cover in these types is indicated by figures from the extensive reconnaissance of the San Joaquin Valley,



FIG. 2. An example of the "annual types"—the transition between grassland and woodland in the foothills of the San Joaquin Valley. Blue oak, *Quercus douglasii*, and interior live oak, *Quercus wislizenii*, may be seen in the background. Annual plants dominate the herbaceous cover in both types.

in 1934. To cite three examples, annuals comprised 94 per cent of the herbaceous cover in the grassland areas, 98 per cent in the woodland, and 93 per cent in the more open chaparral. Perennials are comparatively abundant, however, in some parts of the region diagrammed in figure 1, for example, in rather extensive valley areas where saltgrass is important, and locally in the Coast Ranges where bunchgrasses are prevalent.

Surprising also is the extent to which the native vegetation over vast areas in California has been replaced by plants introduced from the Old World. The reconnaissance of the San Joaquin Valley further revealed that introduced plants (mostly annuals) constituted 63 per cent of the herbaceous vegetation

² This paper is chiefly concerned with the more open phases of woodland and chaparral—not the dense phases which support comparatively little herbaceous growth.

in the grassland types, 66 per cent in the woodland, and 54 per cent in chaparral. Some of the most important introduced species from the standpoint of abundance are *Erodium cicutarium* (20% of total herbaceous cover) and *E. botrys* (14%), *Bromus hordeaceus* (9%), *B. rubens* (9%), *B. arenarius* (2%), *Avena barbata* (2%), *Bromus rigidus* (1%), and *Medicago hispida* (1%). *Hordeum murinum*, *H. gussoneanum*, *Avena fatua*, *Festuca myuros*, and other minor or rare species comprise an additional 1 per cent.³

The annual types are further characterized by the tremendous number of individual plants in the herbaceous cover, and the large number of species.

TABLE I. *Composition of herbaceous vegetation in six grazed pastures, San Joaquin Experimental Range, 1938*

No.	Species	Composition ¹	No.	Species	Composition
		Per cent			Per cent
1	<i>Bromus hordeaceus</i>	17.2	21	<i>Navarretia viscidula</i>	.7
2	<i>Erodium botrys</i>	15.8	22	<i>Pterostegia drymarioides</i>	.6
3	<i>Festuca megalura</i>	10.3	23	<i>Trifolium ciliatum</i>	.6
4	<i>Lotus americanus</i>	5.1	24	<i>Avena barbata</i>	.6
5	<i>Trifolium microcephalum</i>	5.1	25	<i>Trifolium tridentatum</i>	.5
6	<i>Trifolium variegatum</i>	4.1	26	<i>Gilia tricolor</i>	.5
7	<i>Hemizonia virgata</i>	3.1	27	<i>Filago gallica</i>	.4
8	<i>Lupinus bicolor</i>	2.8	28	<i>Montia perfoliata</i>	.4
9	<i>Juncus bufonius</i>	2.6	29	<i>Lotus strigosus</i>	.3
10	<i>Bromus rubens</i>	2.1	30	<i>Linanthus filipes</i>	.3
11	<i>Lotus subpinnatus</i>	1.2	31	<i>Eremocarpus setigerus</i>	.3
12	<i>Plagiobothrys nothofulvus</i>	1.2	32	<i>Lupinus benthami</i>	.3
13	<i>Godelia</i> spp.	1.2	33	<i>Tillaea erecta</i>	.3
14	<i>Daucus pusillus</i>	1.1	34	<i>Lupinus formosus</i>	.3
15	<i>Silene gallica</i>	1.0	35	<i>Pentstemon breviflorus</i>	.2
16	<i>Bromus rigidus</i>	.9	36	<i>Plantago erecta</i>	.2
17	<i>Centaurea melitensis</i>	.9	37	<i>Erodium cicutarium</i>	.2
18	<i>Cerastium viscosum</i>	.8	38	<i>Calandrinia caulescens</i>	.2
19	<i>Baeria chrysosoma</i>	.7	39	<i>Medicago hispida</i>	.2
20	<i>Hypochoeris glabra</i>	.7	40	<i>Layia pentachaeta</i>	.2
				Other species	14.8
				Total	100.0

¹ Composition based on density.

As examples of extreme populations, estimates since 1933 of the dominant forb *Erodium botrys* reveal up to 13,000 young plants per square meter, and as high as 220,000 of *Festuca* on areas dominated by annual species of this genus. The large number of species is illustrated by the San Joaquin Valley range reconnaissance, in which 346 forbs and 79 grasses were recorded; and this number represents only a part of the total number occurring in that large territory.

Some of the most common herbaceous species found in the annual types are given in table I. Although the data in this table are restricted to a description of the composition of the vegetation cover in six large pastures on the

³ Nomenclature follows Jepson's Manual of Flowering Plants of California.

Experimental Range, most of the species listed are common to large areas of the annual types in other parts of California. It is of interest that only 12 species make up 70 per cent of the ground cover, although 109 species were recorded and many others occurred in insignificant amounts.

FLUCTUATIONS IN COMPOSITION AND YIELD

The annual-plant cover is unstable and variable to a surprising degree. Percentages of individual species move back and forth along the scale of relative abundance, from year to year. The amount of vegetation produced annually and the dates of greening and of drying likewise vary. Pronounced changes in aspect occur, both from season to season and during a given season. The species composition not only is different from year to year, but, under complete protection from livestock and rodents, striking shifts in composition can be brought about in two years' time or less; and, by a change in treatment, these trends may be arrested—even partially reversed—in a single season. It is with such fluctuations that the following discussion is concerned.

Fluctuations in grazed pastures. The results of yearly inventories of the vegetation in grazed pastures on the Experimental Range (see fig. 1 for location) indicate that the herbaceous cover is ever changing. In connection with these inventories, noticeable variations in species composition were observed from year to year. The relative yield of herbage also changed. Some of the more conspicuous and significant composition changes are illustrated in table II by 12 species which were selected from table I.

TABLE II. *Changes in herbaceous composition in six grazed pastures, San Joaquin Experimental Range*

No.	Species	Composition percentage		
		1936	1937	1938
1	<i>Erodium botrys</i>	40.6	34.3	15.8
2	<i>Bromus hordeaceus</i>	19.4	30.6	17.2
3	<i>Festuca megalura</i>	16.9	9.3	10.3
4	<i>Avena barbata</i>	2.8	4.2	.6
5	<i>Bromus rigidus</i>	1.4	3.3	.9
6	<i>Lotus americanus</i>	1.2	.6	5.1
7	<i>Hemizonia virgata</i>	.6	.2	3.1
8	<i>Juncus bufonius</i>	.5	.5	2.6
9	<i>Plagiobothrys nothofulvus</i>	.4	2.4	1.2
10	<i>Trifolium microcephalum</i>	.4	.3	5.1
11	<i>Lupinus bicolor</i>	.1	.2	2.8
12	<i>Lotus subpinnatus</i>	.1	.1	1.2
	All other species	15.6	14.0	34.1
Total		100.0	100.0	100.0

Twelve species made up from 66 to 86 per cent of the vegetation in the pastures. Figures for each of the numerous species comprising the 14 to 34 per cent designated as "all other species" also fluctuated, but the recorded differences were small and may have been less than the errors of measurement.

These data are based on square-foot plots distributed at random (at the rate of one per acre in 1936 and 1937, and one to two acres in 1938) on 1,440 acres.

Fluctuations in fenced exclosures. Sharp fluctuations in herbaceous vegetation induced by extremes in treatment are illustrated by the 5-year story obtained from livestock and rodent exclosures at an outpost of the Experimental Range, in the woodland type. These exclosures, one 10 acres in size excluding livestock, and one 50 feet square excluding rodents also, were fenced in 1933. Systematic estimates and measurements of vegetation were recorded in 1933, 1935, 1937 and 1938 at approximately the same growth stage (maximum development) on three plots, one in each of these two exclosures and one in an adjoining grazed pasture. The comparative estimates are summarized in table III. Grazing on plot No. 3 was close and fairly uniform from 1933 to 1936, moderate in 1937, and very light in 1938.

TABLE III. *Fluctuations in composition under different treatments*

Plot	Treatment	Year	Total		Four most abundant species			
			Forbs	Grasses	<i>Ero-</i>	<i>Bromus</i>	<i>Avena</i>	<i>Bromus</i>
					dium spp.	hor- deaceus	bar- bata	
Per cent of cover								
1	Rodents and livestock excluded	1933	98	2	86	1	T	T
		1935	4	96	3	20	72	4
		1937	1	99	0	10	1	88
		1938	20	80	1	10	10	60
2	Only livestock excluded	1933	99	1	80	T	0	T
		1935	15	85	14	75	10	T
		1937	4	96	2	85	8	T
		1938	20	80	0	55	20	T
3	Grazed by livestock and rodents	1933	98	2	82	T	T	T
		1935	79	21	50	5	T	T
		1937	67	33 ¹	50	0	0	T
		1938	43	57 ¹	10	24	T	T

T (Trace) = Values less than 1 per cent.

¹ Includes *Juncus bufonius*.

The marked changes that were observed in the forb-grass ratio in only two years are shown graphically in figure 3. Some of these changes from 1933 to 1935, under all three treatments, were of course due to climate; but the replacement of forbs by grasses is significantly greater in the fenced plots, virtually amounting to a reversal in ratio.

Even more striking evidence of the rapid response of this delicately balanced vegetation to extremes of treatment is afforded by the results of careful removal of accumulated old growth by hand from three alternate strips across the rodent exclosure, leaving the intervening strips undisturbed as checks. This was done in October 1936, just before the beginning of the rainy season and the start of new growth. By the following May sharp contrasts were

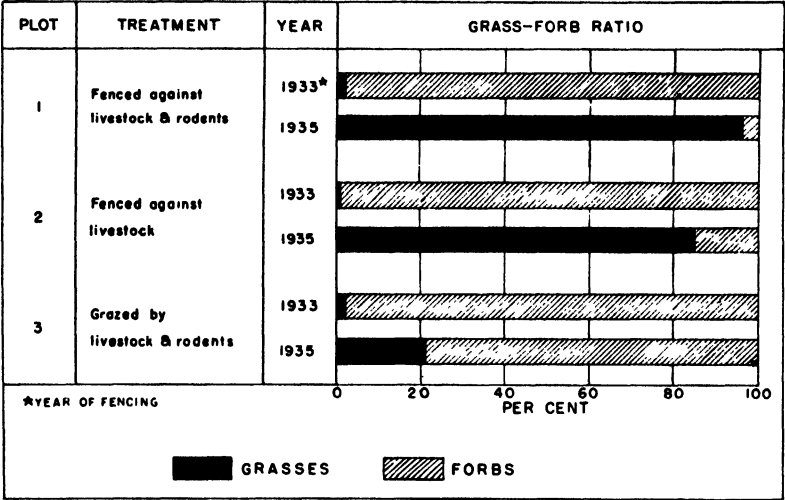


FIG. 3. Comparative replacement of forbs by grasses in two years, under three treatments.

clearly visible from the boundary fence of the enclosure, throughout the length of each division line between strips. These striking differences in composition, by pairs, of cleared and uncleared strips are indicated in figure 4.

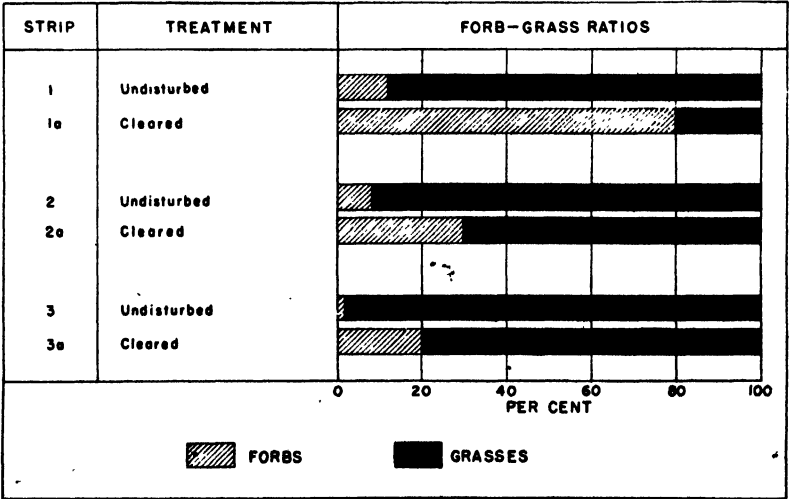


FIG. 4. Increase in forbs from one season's clearing.

This diagram emphasizes the occurrence of a consistently greater proportion of forbs on the cleared strips.

Reexamination of these plots in 1938 revealed still further changes, in comparison with 1937, as indicated in table IV.

TABLE IV. *Fluctuations in vegetation on cleared and uncleared strips in rodent enclosure. Figures in each column represent an average of 3 strips*

Year	1937		1938	
Treatment	Uncleared	Cleared in 1936	Uncleared	Cleared in 1936
Density	.33	.50	.43	.82
Species	Percentage of cover			
<i>Bromus rigidus</i>	69	31	43	4
<i>Avena barbata</i>	14	20	20	17
<i>Bromus hordeaceus</i>	10	10	3	1
<i>Erodium</i> spp.	5	39	4	13
<i>Lupinus bicolor</i>			15	46
<i>Trifolium</i> spp.			10	14
Other forbs	2		5	5
Total grasses	93	61	66	22
Total forbs	7	39	34	78

The relative effect of clearing, which showed up in 1937, the first growing season after treatment, was still strongly evident in 1938. The relatively higher density of the vegetation on the cleared as compared with the uncleared strips was still pronounced. Also, the ratio of forbs to grasses on the cleared strips continued to be relatively greater than on the uncleared. An additional noteworthy point was the big increase in forbs in 1938 on both cleared and uncleared areas, especially of *Trifolium* spp. and *Lupinus bicolor*. In 1937 these species were either absent or represented by so few individuals that they escaped the observer's eye.

Examples of extreme fluctuations in annuals. Contrasts in the growth of annuals in the grassland type were especially impressive in the southern part of the San Joaquin Valley, in Kern County, in 1934 and 1935. In this locality conditions were very unfavorable to plant growth during the 1933-1934 season, in contrast to the following season during which growing conditions were excellent.

The plant cover on seven .25-acre grassland plots, distributed in five localities, was examined and recorded during the course of the range reconnaissance in 1934. The plots were reexamined in 1935. The results of the two examinations are summarized in table V.

TABLE V. *Consecutive seasonal differences in annual vegetation Kern County*

Locality	Number of plots	Height		Density	
		1934	1935	1934	1935
		Inches		Per cent	
Caliente	1	.75	9.0	10	90
Bakersfield	1	.50	3.5	3	40
McKittrick	1	.25	16.0	2	50
Buena Vista Lake	1	.25	5.0	5	60
Lost Hills	3	.44	4.7	3	40
Average		.44	6.8	4	51

The comparative figures in this table illustrate the marked differences in average height and percentage of ground covered by herbaceous vegetation on these plots, from one growing season to the next. The product of height and density, affording a rough index of plant volume, indicates a production of herbage approximately 193 times greater in 1935 than in 1934.

Marked differences in composition of the cover likewise were observed. For example, only 12 species were recorded on the plots in 1934, as compared with twice that number in the following year. In 1934 three species, namely *Erodium cicutarium*, *Lepidium nitidum* and *Bromus rubens*, made up 97 per cent of the herbaceous cover. In 1935, 15 species were needed to make up this amount. The following comparisons are indicative of the most conspicuous changes in the relative proportion of the species from 1934 to 1935. *Erodium cicutarium* decreased from 70 per cent to 29 per cent. A species of annual composite unrecorded in 1934 made up 13 per cent of the cover in 1935, while an annual fescue increased from 1 to 12 per cent. The relative proportion of *Bromus rubens* and *Lepidium nitidum* did not change significantly, although the yield for these species as well as others was vastly greater in 1935. Fluctuations such as these are not uncommon over a period of years in this locality.

Wide fluctuations in herbaceous vegetation, as outlined in the foregoing pages, hold more than academic interest. Directly related as they are to uncertainties in forage supply and soil cover, they complicate range and watershed management. Thus, as a factor in practical land use they have economic importance.

USE OF TENSIOMETERS FOR SOIL MOISTURE MEASUREMENT IN ECOLOGICAL RESEARCH

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The measurement of the availability of soil moisture to plants has long been a serious problem owing to the fact that suitable apparatus has not been developed. During recent years investigators have been turning to a newer concept of soil moisture which is concerned with the force with which the soil retains its moisture. At the same time valuable improvements have been made in instruments for measuring this force. It is the purpose of this paper to bring one of these instruments, the tensiometer, to the attention of ecologists and others who are concerned with soil moisture as it affects plant growth and distribution. Some data will be presented to demonstrate the value of these instruments in solving soil moisture problems.

The term tensiometer was applied by Richards and Gardner ('36) to this instrument which measures the capillary tension¹ of soil water over the range from zero to about one atmosphere. Since capillary tension is a function of the percentage of water in a soil, tensiometers are very useful as continuous reading instruments for estimating moisture content of soil in place. However, as will be seen, the capillary tension value is in itself an important index of soil moisture, possibly more useful than percentage of moisture.

The principle of tensiometers is as follows: a porous vessel (referred to as tensiometer cup) of clay or other ceramic material is buried in the soil to the depth at which moisture conditions are to be measured; it is connected by means of copper tubing to a manometer or other tension indicating instrument located nearby. The system is filled with water and sealed, thus forming a continuous column between the manometer and porous vessel. This water communicates with the soil water through the pores in the vessel and any change in capillary tension in the soil is accompanied by a flow of water through the pores until the tension inside equals the capillary tension in the soil surrounding the cup. The magnitude of this tension is measured by the manometer. The amount of flow which takes place is determined by the volume change necessary to bring the manometer to the new reading.

The porous cups must have pores fine enough to prevent the passage of air at high tensions when the cup is wet, yet coarse enough to permit fairly rapid flow of water. Those used in the experimental work reported herein were shaped like test tubes, .875 inches in diameter and 3.5 inches long. They

¹ Sometimes called "soil pull," "pressure deficiency," and "suction pressure."

were made by the author from a mixture of Hanover Clay (a commercial air-floated pottery clay) and Dunkirk Clay (a naturally occurring glacial lake-laid material), fired at 950° C. A satisfactory form is now being produced commercially,² which simplifies tensiometer construction.

This instrument is capable of measuring tensions to about 65 cms. of mercury with considerable accuracy. The tension at the wilting percentage is about 15 atmospheres, or somewhat over 1000 cms. of mercury.³ Unfortunately, therefore, tensiometers are applicable over only a comparatively small part of the range of tensions existing in soils. However, expressed in terms of percentage of water, this range of applicability represents in most cases, probably, 75 per cent of the possible available water; furthermore, the most rapid water movements in soils occur within this range. The tensiometer data in the literature are evidence that in many situations these instruments will give continuous measurement of capillary tension throughout the growing season.

Various forms of tensiometer installations have been described in the literature (Heck, '34, Richards and Gardner, '36, Richards and Neal, '36, Rogers, '35), so detailed description need not be given here. The form used by the author to obtain the data which appear in this paper was very similar to that shown in figure 1 of the paper by Richards and Neal. The glass air trap was not used but is to be recommended highly for easy detection of entrapped air. Figure 1 shows the above-ground parts of two field installations which were used in a plantation of red pine. The shelter housed three manometers made of 1.5 mm. bore barometer tubing, supported on a panel of 0.25 inch Masonite Prestwood. The scale consisted of millimeter cross section paper secured with shellac to the panel in back of the manometer tubes. The lower end of each tube extended to within .125 inch of the bottom of a 10 cc. shell vial which served as a mercury reservoir. A small error is present where this design is used due to changes of level of mercury in the reservoir. The magnitude of this error can be greatly reduced by the use of a large diameter reservoir.

Recording vacuum gauges can be substituted for the manometers and possess the advantage that they give a continuous record for one week without attention, while manometers or indicating vacuum gauges should be read daily. The recording gauges are, however, quite expensive as compared with the manometers.

The direct readings from the mercury manometer do not express the capillary tension in the soil in units of mercury column since the mercury is partially balanced by the water which connects it to the porous cup. The water column can be considered in two portions—that below the level of the mercury reservoir and that which extends above it to the top of the mercury column. The first portion is constant and can be corrected for by either

² Obtainable from the General Ceramics Co., R. C. A. Bldg., New York City.

³ This value is an average adopted by Schofield ('35)

adjusting the zero point on the scale or by calculating the error and applying a correction to each reading. The second portion equals the height of the mercury column and therefore is variable. In the present case, correction has been made on the graph by expressing tensions as centimeters of mercury $\times 1.08$. It would be much more convenient if scales were available which were graduated on the basis of 1.08 cm. divisions. Direct manometer readings could then give tensions expressed in centimeters of mercury which exist at the porous cup in the soil. A further correction is necessary if small bore tubing is used for the manometers—that for the capillary depression of the mercury. This also is taken care of by properly adjusting the zero point of the scale used.



FIG. 1. Tensiometer installations in a red pine plantation.

Temperature changes may affect the results in two ways: first, they change the actual capillary tension in the soil and, second, they alter the volume of water in the connecting tubes causing errors in the manometer readings. In the present work this difficulty was largely avoided by taking readings before 9 A.M., that is, immediately following a period during which the temperature had been comparatively uniform.

In cold climates, there is danger that porous clay cups will be damaged by freezing water if they remain in the soil throughout the winter season. If it is feasible, they should be removed during the fall season. Rogers ('35) has described a form of clay pot which was designed to avoid this difficulty.

THE SIGNIFICANCE OF CAPILLARY TENSION

It is common knowledge to all who have been concerned with soil moisture that mere percentage of moisture, based either on unit weight or unit volume of soil, may tell nothing concerning the availability of that moisture to plants. It is necessary to interpret such data in terms of certain single-valued properties which depend on the nature of the individual soil concerned. The common procedure is to relate the percentage of moisture to some previously determined soil moisture "constant," such as wilting percentage, moisture

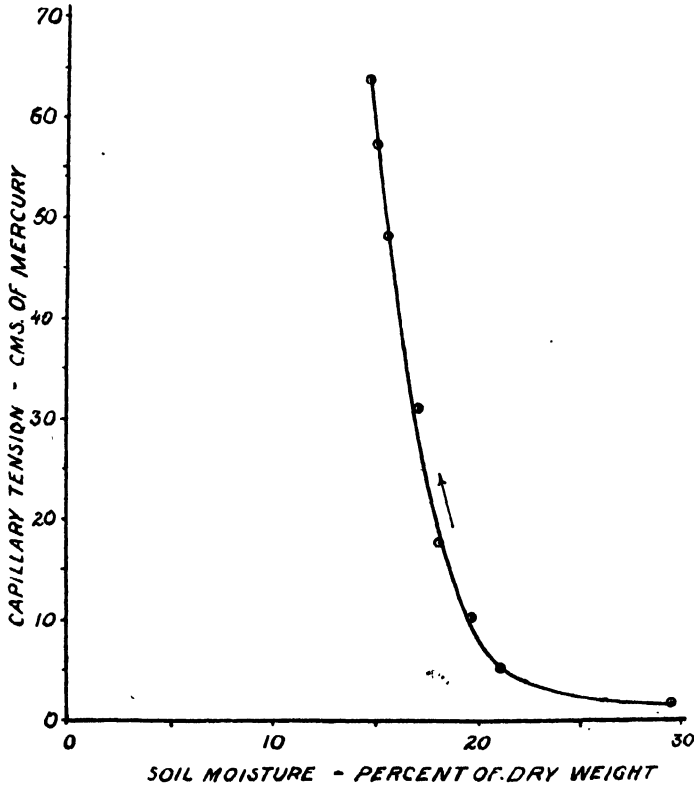


FIG. 2. Tensiometer calibration of a soil sample taken from the 18-inch depth near plots 12, 14, and 20.

equivalent, or water-holding capacity. For example, knowing the wilting percentage of a soil and the amount of water which is present at a given time, one can calculate the amount of available water present. Another commonly used index of soil moisture is relative wetness—the moisture content expressed as percentage of moisture equivalent. Likewise, the water-holding capacity is often used as a basis for expressing soil moisture conditions, but it is probably the least useful for such purposes owing to the lack of standardized procedure for its determination. The use of any of these

methods for determining moisture trends in a given plot of soil necessitates the removal of large numbers of soil samples which must be transported to the laboratory, weighed, dried, and reweighed. Such a procedure is very laborious and time consuming. Furthermore, the data which are obtained are not an accurate measure of the actual tension which the plant must exert in order to extract water from the soil under the existing conditions. They represent, in effect, an attempt to approximate the value which tensiometers give directly—an expression of the force with which water is being held by the soil. This lack of means for continuous measurement of soil moisture and its “availability” has stimulated the development and increased use of tensiometers.

As stated above, capillary tension in a soil is a function of the percentage of water in that soil. In figure 2, which shows this relationship for one soil, it will be observed that the relation is not linear but rather of an hyperbolic nature. At a point somewhat below saturation the tension is zero, increasing gradually at first as the soil water is decreased but soon beginning to increase very rapidly. In this soil a quite abrupt change in rate occurs within the range from about 20–24 per cent moisture. The shape of the curve and its position with respect to percentage of moisture varies with the soil concerned; the curve for a more sandy soil would lie to the left of the one shown and that for a more clayey soil on the right.

USEFULNESS OF TENSIO-METER DATA

Interpretation of capillary tension data is commonly made with the assumption that they are related to the availability of soil water to plants. Soluble salts exert an osmotic effect which is not measured by tensiometers but this is extremely small in most soils and capillary tension represents, for all practical purposes, the force which opposes the absorption of water by plants. Hence the absorption force of the plant must exceed this value in order to effect removal of soil water.

Another feature of tensiometers is that they give continuous measurements of soil moisture without any disturbance of the soil after installation of the instruments. In certain types of studies this is highly important.

The data obtained with the use of tensiometers represent not only capillary tensions but they can be converted into percentages of moisture by the use of a graph similar to the one shown in figure 2, making possible the use of such data for calculating total and available water supplies. This calibration curve is obtained by determining the percentages of water present in the soil at various respective tensions and plotting the results. The curve obtained is a calibration of the tensiometer for that particular soil. The data can be obtained either in the field by periodic sampling in the vicinity of a tensiometer which is placed in a representative soil area, or by removing a single sample of soil to the laboratory and artificially adjusting the moisture content. More

detailed instructions for these operations are given by Richards and Gardner ('36) and by Richards and Neal ('36). The shape and position of the curve varies somewhat depending on whether the soil is being wetted or dried at the times of measurement. If only one of such curves is to be obtained the drying procedure should usually be used since investigators are more frequently concerned with soil moisture at times when drying processes prevail than when the soil is being wetted. The data for the curve shown in figure 2 were obtained by saturating a sample of the soil in a number 3 tinned can and then drying by removing water through a porous cup with controlled tensions. The soil sample was obtained in such a way as to retain the field structure as nearly as possible.

During the summer of 1937 the author used tensiometers in connection with a trenching⁴ study of forest soils. Some of the data are of interest here in that they point out some of the uses to which these instruments can be put. Figure 3 shows the tensions which occurred⁵ in three differently treated plots throughout a large part of the growing season. Each plot was a milacre in area; in each were placed three tensiometers with the cups at respective depths of 2, 8, and 18 inches. These depths were chosen for the following reasons: 2 inches was the approximate thickness of the organic layer, which means that the first cup lay at the junction of the organic layer with the mineral soil; the 8-inch depth was chosen as representing the zone of greatest concentration of tree roots; 18 inches is about the greatest depth to which many roots extended since the soil below that was extremely compact and sometimes affected by a perched water table. The 2-inch cup lay in a nearly horizontal position while the two deeper ones were only slightly away from vertical.

The area upon which these plots were located was occupied by an even-aged stand of mixed hardwoods of the red oak-basswood-white ash type.

Plot 12 was surrounded by a trench, dug to a depth of 22 inches and immediately refilled, in April 1937. No large trees were included within this plot—only herbaceous and small woody plants, including tree reproduction. Plot 14 was a check, receiving no treatment whatever. Plot 20 was similar to plot 14 but was kept moist during rainless periods by additions of water. It also received 0.4 pound of sodium nitrate at the beginning of the growing season but that treatment is unimportant to the data considered here. The intention at first was to keep it as moist as the trenched plot but the large trees absorbed water so rapidly that this was found to be impracticable. An arbitrary limit of 30 cms. tension was then set and water applied whenever the tension reached this value. As a result the tensions on this plot rose only

⁴ The term "trenching" refers to the isolation of a plot of soil by digging a trench around it for the purpose of cutting all roots which enter it from plants outside.

⁵ It must be borne in mind when one interprets tensiometer data that percentage of soil moisture and capillary tension are inverse functions, i.e., a rising tension indicates a removal of moisture from the soil and vice versa.

occasionally to values greater than 30 cms. and then only for brief periods. Comparison with the tensions reached in the nearby check plot indicates the effects of irrigation.

In plot 12 only the lesser vegetation of the forest was represented and root competition from large trees was eliminated by the trenching. The effect of this treatment is apparent when one compares the capillary tension records of plot 12 with those of plot 14 (check). Throughout almost the whole growing season the tensions existing in the trenched plot were very much lower than those in the check plot, indicating a higher moisture content.

The results of this investigation, then, suggest at least two important applications of tensiometers:

1. They indicate the times at which water must be added in experiments where the water supply in the soil is being artificially maintained. This application should be of importance in the nursery and greenhouse as well as in the field.

2. They provide a means for measuring the effect of a given treatment on soil moisture (such as trenching, in this case).

The records shown in figure 3 serve as illustrations of additional types of information which are important in many soil moisture investigations. First, they indicate capillary gradients, showing whether moisture tends to move up or down in the soil; furthermore, they give some idea as to the magnitude of these gradients; in some instances they show the direction and rate of water movement. In plot 14, for example, the rain which occurred on August 9 was reflected at the 2-inch depth by an immediate drop in tension but a corresponding drop was not apparent at the 8-inch depth and 18-inch depth until later, indicating something as to the rate of downward penetration. If continuous recording apparatus had been used, the curves would show the exact time at which the percolating water reached each successive depth. Second, tensiometers can be used to indicate the approximate level of the free water table in a saturated soil. When a head of free water exists above the tensiometer cup a pressure rather than a tension exists at the cup. This pressure can be measured on the manometer. Such a condition occurred in plot 20 on August 28. In other plots, not reported here, it occurred several times during the season. Third, it is of interest to note that at the 2-inch depth there was a tendency for the tension not to rise above 30 cms. There are not sufficient data available to justify speculation as to the possible significance of this fact.

One might suggest a number of possible further applications of the tensiometer method. In certain regions it might be very helpful in erosion experiments, as indicated by the work of Richards and Neal ('36) in Iowa and of Richards and Lamb ('37) in New York. Tensiometers may be useful to plant physiologists who are studying the effects of soil moisture on various phases of plant growth and behavior. Results so far available suggest that the method is particularly well suited to forested soils of the humid regions

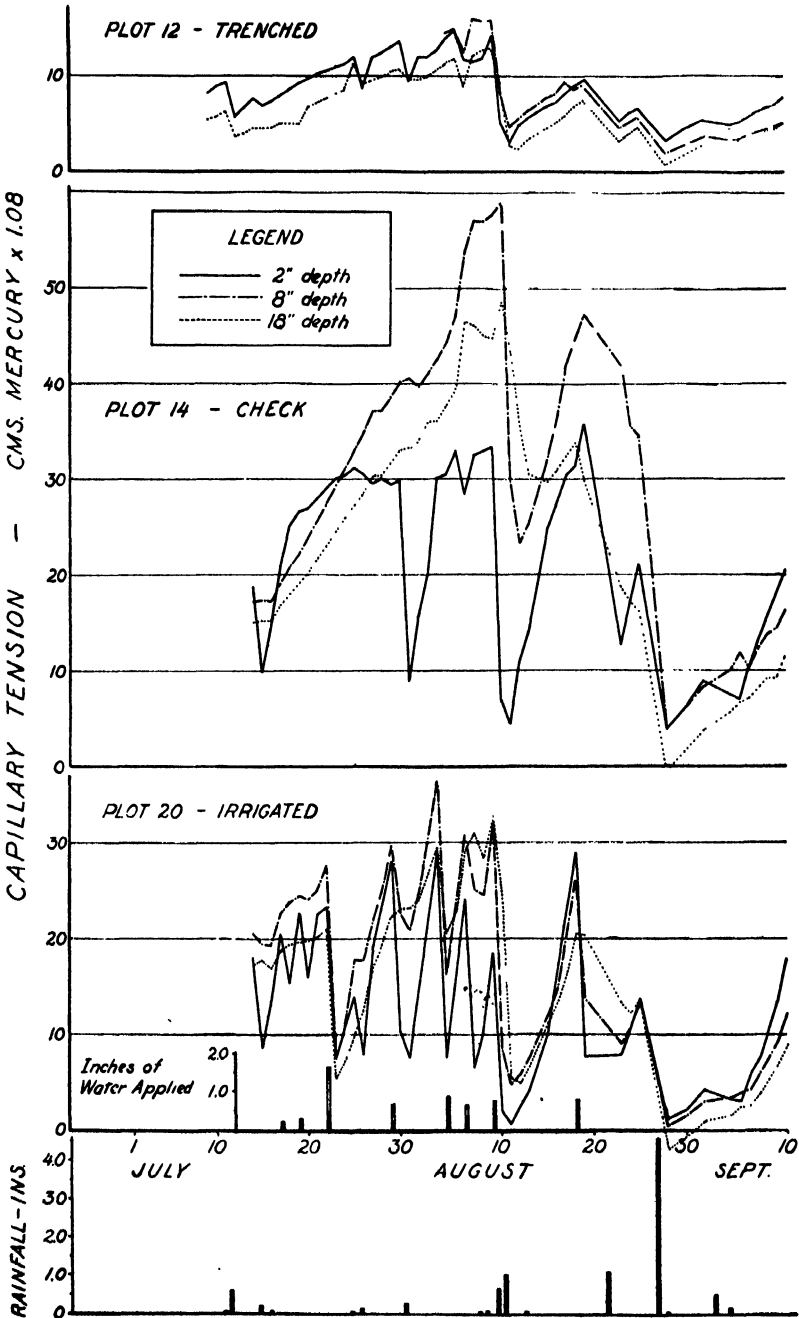


FIG. 3. Tensiometer, rainfall, and irrigation data for plots 12, 14, and 20 taken in 1937.

since the tensions reported in these seldom exceed the limitations of the instrument. The graphs of Richards and Lamb ('37), figure 2, show lower tensions in the forested plot with 27 per cent slope than in a nearby fallow plot with only 20 per cent slope. Presumably this difference can be attributed to a greater absorption of rainfall by the forest covered soil.

Livingston and Norem ('37) have questioned the usefulness of static methods (which include tensiometers) for determining the moisture status of a soil, on the basis that they tell one nothing as to the water supplying power of the soil. This, they say, is the factor which determines whether or not a plant is able to absorb enough water for life processes. The latter statement appears to be valid except for one fact—that plant roots do not rely entirely on conduction of water through the soil but are capable of growing into regions of lower tensions; they constantly renew the available supply of water by growing toward it. It is true that tensiometers do not measure water supplying power, as such; but since the latter is a function of capillary tension for a given soil, some indication is obtained of its relative value by inspection of tensiometer data. If the soil points designed by Livingston measure directly the water supplying power of soils, however, they should prove of great value in soil moisture studies.

The relationship between capillary tension and such ordinary soil moisture constants as moisture equivalent and field capacity needs more study to enable us to interpret data of one type in terms of the other. Data obtained by Schofield and Botelho da Costa ('35) by the freezing point method indicate that the moisture equivalents of various soils represent a range of tensions from 23 to 66 cms. of mercury. The moisture equivalent of the soil whose calibration is given in figure 2 (obtained from a depth of 18 inches near plots 12, 14, and 20) was about 21 per cent, which corresponds to a tension of 5 cms. of mercury. It appears probable from the data available that the moisture equivalent lies within the range of soil moisture in which tensiometers can be used. There is need for a great deal of research on this phase to permit coordination of the past work on soil moisture and the newer point of view involving energy relations, whether the latter be expressed as capillary tension, freezing point depression, or vapor pressure.

There is a distinct lack of moisture data for forest soils. In the more humid regions of the United States the idea has been frequently expressed that in seasons of normal rainfall forests do not suffer from lack of moisture. This attitude seems to result primarily from two circumstances: first, the fact that in such periods it is not common to see trees wilted or dying from lack of moisture and second, there has been available no satisfactory way of measuring soil moisture in terms of availability. Tensiometers offer a convenient means for studying a very useful range of available moisture, although we may find that water does not limit growth of plants when within this range.

SUMMARY

1. A brief description of tensiometers and the principles of their use is presented.

2. Some outstanding characteristics of these instruments are given and may be summarized as follows:

a. They measure the force with which water is being held by the soil, without reference to the nature of the soil.

b. Their readings can be converted into percentage of soil moisture by proper calibration.

c. The apparatus gives continuous readings without disturbance of the soil after installation; designs which give continuous records have been found practicable.

d. Readings of two adjacent tensiometer cups give a measurement of the direction and magnitude of the capillary gradient.

e. Since they utilize manometers, these instruments are limited in range to one atmosphere of tension; this represents a soil moisture range from saturation to a point somewhat below the moisture equivalent.

f. The conducting system of a tensiometer must be absolutely air tight; it must also be kept free from gas pockets.

g. The porous clay vessels are susceptible to damage by freezing so in cold climates should be removed from the ground at the end of the growing season.

3. Some data obtained by the author are presented as evidence of the usefulness of tensiometers to those doing ecological research.

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REVIEWS

BIOCLIMATICS ¹

(The What and Why)

The science of "bioclimatics," as developed by Dr. Hopkins over a period of about forty years, is, in brief, an attempt to correlate the seasonal phenological phenomena of plants and animals with the various elements which make up the climate of a region. These elements, as studied up to the present time, include temperature (with especial emphasis upon the annual mean and the means of the coldest and warmest months) and rainfall, but it is admitted that as other elements of climate are studied more in detail the science will become progressively more exact.

Starting out with the question of temperature, it has been customary in the past to divide the regions of the earth into five large zones—two arctic, two temperate, and one tropical. These are separated from each other by imaginary lines running around the earth parallel with the equator. According to the principles of astronomy ("astronomic law"), it is to be expected that the life zones, like the climatic zones, would fall into belts varying gradually from each other as one passes from the equator to the poles.

When one actually observes the phenomena, however, not only of climate but of life, one finds that the lines which go through points representing equal life phenomena do not run parallel with the equator across the continents but instead they run from northwest to southeast across the land masses. This is true both in the northern and in the southern hemispheres. Such lines are here called *isophanes*, and, in general, it has been found practical to draw these lines at an angle of about 30° with the parallels of latitude in such a fashion that the isophanes depart 1° of latitude from the parallels of latitude for every 5° of longitude across the continents. Because the 100th meridian (both east and west) lies in the center of the great land masses, this has been taken as the center for drawing the isophanes. This means that the isophanes and parallels of the same number cross each other on the 100th meridian.

If one crosses the continent from east to west in a northwesterly direction along the isophane he is, therefore, passing through regions where the seasonal phenomena in the life history of an organism take place at the same time of year, assuming that the positions on the isophane are all at sea level. In order, however, to correlate the phenomena at different latitudes and altitudes so that those at any one spot can be compared with those in any other place on the earth's surface, some relation must be established between these units of al-

¹ Hopkins, A. D. 1938. Bioclimatics; A science of life and climate relations. U. S. Dept. Agri. Misc. Publ. 280. 188 pp.

titude, latitude, and time. Experience has shown that 1° of latitude (or isophane) equals 400 feet of altitude or 4 days of time, and thus throughout this entire work great emphasis is laid upon the fact that *bioclimatics is a coordinating science* depending for its chief results upon a coordination of the three units of time, horizontal distance, and altitude.

Thus, if it is known at what time a certain species of flower opens at sea level at latitude 40° N., it can be determined with a high degree of accuracy at what time it will open at latitude 30° N. and at an altitude of 2,000 feet. With these coordinate relations established between time, distance (in latitude and longitude), and altitude, it is possible to set up for each phase in the life history of every organism a date (constant) when it *should* take place.

It is obvious, however, that if a science of *world bioclimatics* is to be established, a base point must be set up as the standard of reference for these phenomena. For this purpose, the author has proposed for the "intercontinental base" a region in West Virginia near Parkersburg, centering in an area called the Kanawha Farms. While this was set up primarily because it is the region with which the author is most familiar and in which he has taken phenological data over a period of about 40 years (this section probably has been worked more intensively from a phenological point of view than any other in the world), it so happens that the region is located in an ideal situation for a base station, being on one of the tributaries of the Ohio River in a temperate climate, transitional in character, between the Appalachian Mountains and the Mississippi Basin. The region is described in detail, and the numerous data obtained there are summarized in various sections of this work.

After the author has given a great many illustrations (called "test examples") to show that the phenomena of life and climate follow bioclimatic law (that is, the isophanes) rather than astronomic law (that is, parallels of latitude), the next step was to establish for many different types of phenomena the "bioclimatic constants." In these tables of constants are given the dates, altitudes, latitudes, etc. which would be required according to the coordinated relations of time, temperature, and distance; if the phenomena followed absolutely the bioclimatic law. We know, however, that they do not in every case follow these laws exactly, and at this point there is developed the idea of the variation from the constant as a key or index to the cause of the variation. This very ingenious development of the science of bioclimatics is an attempt, therefore, to establish a scientific basis whereby *if one knows the variation of a phenomenon from the expected constant, he may derive some clue as to why the variation has occurred.* A large part of the work is devoted, therefore, to the determination and "interpretation" of the variations from the constants; and the many formula used throughout the work in the various examples are given in order to aid the reader and researcher in these interpretations.

In Part II is developed the theory and principles of the bioclimatic zones. Keeping in mind always that the ultimate criterion of the climate of a place

from a biological point of view is the actual behavior of the organisms on the spot, it is possible to classify each general region, specific region, or even *each farm* on a bioclimatic basis, so that if one knows the elements of the climate over a period of years, as taken both from the meteorological records and from the biological phenomena, one can classify every region into one of the 3 major and 15 minor zones, and still further into one of numerous zonal types. Similarly, the seasons are determined by the climate and not by a date on the calendar.

Since up to the present time, temperature records are much more complete than those of any other climatic phenomenon, temperature has been emphasized more than any other climatic element, although it is realized that precipitation, light, etc. must be taken into account and that, as our knowledge of these elements increases, the zonal classifications will become progressively more accurate. With zones based primarily upon temperature, however, great progress can be made because, as is well known, temperature is the chief determiner of the range of plant and animal species. It is for this reason that the *a* (annual mean temperature), *w* (mean temperature of the warmest month), and *c* (mean temperature of the coldest month) are emphasized so much in the determination of the zones and zonal types. Using the author's system of classification of zonal types, it is possible to classify bioclimatically (and consequently from the viewpoint of the flora and fauna) minute areas, and thus one can compare a small region (or farm) on any continent with a similar area on any other continent.

The chief principles involved in the system of the science of bioclimates, therefore, are: (1) the establishment of the isophane as a more correct index to biological phenomena and climate than the parallels of latitude, that is, the isophanes more nearly represent lines of equal climatic and biological phenomena than do the parallels of latitude; (2) the coordination between time in days, altitude in feet, and distance in degrees of altitude (or isophane) and longitude into one unified system, by which it is possible to compare phenomena anywhere over the surface of the earth with a standard ("The Intercontinental Base Station") or with each other; (3) the development of tables of constants to serve as standards for measuring variations from the constants, which in turn serve as indices to the causes of these variations; and (4) the subsequent determination of bioclimatic zones and zonal types, which enables one to classify each local spot and consequently to *predict* what types of plants and animals might be expected to thrive there.

The science of bioclimatics thus solidly established seems (1) to open up an extremely practical field of research, the surface of which has hardly been scratched, and (2) to give promise of being of great service to applied agriculture in many lines, only a few of which may be mentioned here:

1. *In economic entomology*, it is important to know the possibilities of the spread of an insect. Since each phase of an insect's life history is related more or less intimately with environmental phenomena, such as climate or the

location of its food supply, accurate and detailed information on these points both in the region of its possible invasion and in the region from which it comes will be of enormous practical value in predicting possible damage, in predicting possible enemies, and also in predicting regions from which its enemies may be obtained, that is, in establishing general control measures.

2. *In plant pathology*, where many of the statements hold for plant diseases as for undesirable insects, bioclimatic principles could also doubtless be of great service.

3. *In forestry*, in connection with establishment of forest areas using either native or exotic trees, a knowledge of (a) the intimate relations of the trees to climate and (b) the climatic elements of the region, carefully analyzed according to bioclimatic principles, would result in avoiding much of the waste of empirical "cut-and-try" methods.

4. *In agronomy and horticulture* the same (or similar) principles hold as in growing tree crops, *i.e.*, as in forestry. The value of such studies is also seen in the question of plant introductions and the growing of exotic plants. A careful detailed analysis of the climatic elements of the region from which the plants come, along with that of the region where it is hoped to grow them, would save much time and effort.

5. *In soil science*, likewise, there is a great field of comparative soil classifications opened up here in connection with plant geographical studies. The local soils should be correlated with climate and the local biota, but this field is barely touched upon in Dr. Hopkins' work.

The science of bioclimatics thus seems to open up an extremely practical field of research and to give promise of being of great service to applied agriculture in many lines. Admittedly there is much work yet to be done, but a start has been made. While the book in many spots is rather formidable reading, it is no more so than any work which attempts a mathematical analysis of biological processes. It is also true that the work in spots seems a bit verbose and repetitious with "redundant superfluities," but the author, evidently imbued by the desire that he should not be misunderstood, felt that some repetition was justified in the interest of clarity and by the newness of the field. At any rate, monuments frequently bear similar inscriptions on more than one face, and both Hopkins and the ecological sciences are to be congratulated upon the appearance of this pioneering monumental work. The student who carefully follows the author's ideas throughout these pages will be well repaid.

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THE LEGUMINOUS PLANTS OF WISCONSIN¹

This is a luxurious publication complete with excellent photographs and drawings (the latter by Dr. Richard I. Evans), and numerous maps showing detailed distribution of the species not only in Wisconsin but throughout their entire range in North America. It goes without saying that the treatment is thorough from a taxonomic point of view, with basic notations as to actual types. For the ecologist this work is also of exceptional interest in the illustrations of leguminous pods, showing various types of structure and dehiscence, and the keys—departing from the conventional form and here including individual keys based on seeds or fruits as well as on flowers. There is in addition a treatment by Catherine Mose of epidermal outgrowths as seen in the various species of Wisconsin Leguminosae—a valuable addition to the excellent studies on plant trichomes by P. G. E. Theorin which appeared in *Arkiv för Botanik* 1: 1903, and in several succeeding volumes of the same publication. From the viewpoint of plant geography one is impressed by the large number of species—such as *Astragalus caryocarpus*, *A. neglectus*, *A. alpinus*, *Cassia medsgeri*, *Desmodium bracteatum*, *D. canescens*, *Lespedeza virginica*, *L. repens*, *L. procumbens*—which are exceedingly local, and in some cases known from only a single location within the State. *A. caryocarpus* seems connected in its distribution to the postglacial Lake Grantsburg. Secondly, the marked restriction of certain species to sandy and prairie soils—e.g., *Baptisia leucophaca*, *B. leucantha*, and *Psoralea esculenta*. “The Pomme de Prairie [*P. esculenta*] occurs at several places in St. Croix and Pierce counties, where bits of original prairie have survived, either at the tops of bluffs along the Mississippi River or on isolated hilltops in cultivated land which are uncultivated because of their stoniness or steepness, and which have not been pastured because of their isolation, surrounded as they are by crop land (Fig. 36).” Finally, and of greatest interest, the restriction of certain species to the driftless area, such as *Lespedeza leptostachys* and perhaps typical *Tephrosia virginiana*.

It is hoped by the reviewer that this publication will be only the first of a series dealing with difficult plant families. Limited to a restricted area, such treatments can be brought to a successful and complete termination, as Dr. Fassett has done in his volume on the Leguminosae.

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BROOKLYN BOTANIC GARDEN

¹ Fassett, Norman C. 1939. Leguminous plants of Wisconsin. *Univ. of Wis. Press.* \$3.00. 157 p., 24 pl., 60 fig., 197 maps.

AN ECOLOGICAL AUDIT ¹*Contents*

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The conference on plant and animal communities at Cold Spring Harbor grew out of the long continued interest of the Biological Laboratory in ecological teaching and research. It was arranged by a committee composed of Stanley A. Cain (chairman), William A. Castle and Herman T. Spieth.

It is difficult to decide how to review this significant volume of proceedings. I am tempted to consider the articles one by one and exhibit their strengths and weaknesses piecemeal. If that possibility is rejected it is certainly not because down that path lie strengthened personal friendships and potential animosities but rather because that plan adequately developed would yield too long and tedious a review. Also there would be a loss of certain unities; at least there are unities among these papers that are picked up by the tolerant eye of one accustomed to see something of the quasi-organismic in biotic communities in nature. There are obvious disunities also, but by consciously shifting ground from time to time I find myself able to agree with most of the major points of view expressed, no matter how divergent.

The different contributions are uneven in almost every respect. Papers that are concerned more strictly with animals, for example, range from the scholarly summary of a situation by Emerson through the excellent introductions to their different subjects by MacGinitie and by Park to the more restricted summary by Tinbergen and the less than adequate treatment by Eggleton. If the papers on plant sociology seem at times to be fuller of words than of meat, that may be because I am merely an outsider and not a student of that aspect of ecology.

¹ **Just, Theodor** (Editor). 1939. *Plant and Animal Communities*. Comprising the proceedings of the conference on plant and animal communities held at the Biological Laboratory, Cold Spring Harbor, 1938. Reprinted from the *American Midland Naturalist*, 21 (1): 1-255. Notre Dame, Indiana. \$2.50.

At the outset let it be understood that in my opinion this volume should be required reading from cover to cover for every research worker in ecology in the world and for all serious beginners interested in any phase of the subject. Some of the former might have their horizons widened and some of the latter, not yet fully committed to an ecological career, might be forewarned concerning the chaotic, loosely-knit field they are thinking about entering.

This conference represents the first ambitious attempt to arrange a general public stock-taking of ecology. It was apparently notably successful—certainly as regards frankness of expression, both in the formal papers and in the less formal discussion. It is a pleasure, particularly to one who remembers the evangelical tone when two or more ecologists foregathered some decades ago, to find the frank skepticism about every aspect of ecology except the value of the subject itself; on that point there was no dissenting voice.

Most of the long-held ecological tenets were called in question. Conard apparently doubted the importance of succession (most clearly on p. 90). Gleason (p. 93, p. 107, p. 108) questioned the existence of an association of plants in any quasi-organismic sense. Lippmaa argued that the unistratal plant communities make a satisfactory unit and Cain rejected a logical application of these "unions" to form the so-called twin associations of the Russians (p. 162 ff) and concluded (p. 176): "There is a tremendous gap between the 'stand' and the Clementsian 'association,' two units which all ecologists are willing to recognize. Between these small and large units lie complex problems of community taxonomy."

This hunt for a satisfactory system of "community taxonomy" is a central and recurrent note in the botanical papers. An onlooker is tempted to advise that ecologists escape from attempting to make practical application of classificatory concepts which seem essentially inapplicable except under more or less local conditions by taking a lesson from Darwin's definition of a species (*The Origin of Species*, p. 30): "Nor shall I here discuss the various definitions that have been given of the term species. No one definition has satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species." This situation did not stop taxonomists from working with the species concept fairly accurately. Similarly it seems to me to be good strategy to postpone for the present attempts to get a universal, all-inclusive and all-exclusive definition of a unit ecological community and systems for their classification, meantime continuing their study.

Evidently the problem of classification of ecological communities of animals is much more complex; so much so that animal ecologists have scarcely begun seriously to work toward possible solutions. Except in their largest aspects and excepting again Carpenter's somewhat unconvincing presentation of the essentially sound concept of the biome, bio-communities received lip-service only.

In many ways the conference was dominated by those who were not present. The ideas of Clements, Shelford, Braun-Blanquet, Juday, Elton and Lorenz and others gave form to the discussion. This is not to say that Lippmaa, Emerson, MacGinitie, Park and Gleason, to name no more, did not have real contributions to make, the more valuable the closer each came to his own field of special study. While not in the confidence of the committee on arrangements, I do know that some present were among those first invited to participate. Others invited were unable to take part because of illness, pressure of field work or for other reasons. One eminent ecologist of my acquaintance with whom, unfortunately for me, I have never been closely associated, refused to take part because he could not see the use of presenting his ideas one day only to have them negated the next day by another prominent speaker. Perhaps the real success the conference achieved was a result, at least in part, of the absence of those who might, and one would think off-hand, should have been present. The participants averaged much younger than if the great pioneers had been present and perhaps were more objective and free on that account.

Few of the speakers became over-involved in terminology, a morass in which the conference might readily have become hopelessly bogged. MacGinitie recognized (pp. 28, 51) the confusion in terms in ecology, especially in animal ecology. The inclusive system of Clements was apparently not in good standing among those present. Yet as Cain pointed out (p. 175), "Clements has a different term for a different thing" and earlier (p. 150), "Irrespective of how widely his concepts and terminology are accepted, he has evolved a philosophy, a grasp of principles, and a terminology which meet nearly every emergency."

One of the difficulties with ecological terminology is the frequent attempt to use in a new sense a good general English word which already has an established meaning. Thus it will take years to work "predominant" around in ecological literature to mean what the dictionaries say it should. Carpenter (p. 80) uses this word apparently in the sense introduced by Smith (1929) and Shackleford (1929) although Shelford, under whose influence this use originated, has apparently dropped it (private communication) in favor of "prominent," and prominent, without knowing for the moment just how prominent an animal might be, was apparently what "predominant" was intended to convey. The problem of an adequate, comprehensive, usable, minimal terminology has not been solved by ecologists. Terminology is not to be successfully established by fiat at either a world congress or at an informal conference; widely usable terminology, like other language growth, must come slowly and by development; this particular gathering did not seriously undertake its consideration.

Many of the problems discussed, particularly by phyto-sociologists, would be nearer solution if we had available some reliable and adequate methodology for collecting, analyzing and interpreting statistical data concerning the com-

position of natural communities. From such treatment, used of course with sense and judgment, we might hope to accumulate coefficients of association of different plants and/or animals. This is by no means a new idea; it was not seriously discussed at the conference. Park's adequate but brief discussion of statistics in connection with populations excepted, this aspect was mentioned only to quote an opinion of its inadequacy (e.g. Cain, p. 148).

The discussions included after each paper help give point to the preceding presentation. The selection of this material for printing seems to have been the chief function of the editor and the result does him credit. The editorial duties did not include making of an index and an index is needed by any reader who takes the book seriously and by any person who wants to use it as reference material; in short by any one who takes up the book. The proof reading also leaves much to be desired. Usually the meaning is clear; however, on p. 56 a line or more is omitted and in the footnote on p. 159 I suspect *cull* was meant in place of *call*. The print is discouraging, especially so in the discussions, and the whole appearance of the volume does not invite favorable comparison to the Cold Spring Harbor Symposia on Quantitative Biology which the relative quality and significance of the material warrant. However, like much of ecology, one is reminded that in the words of a revised adage, "What is worth doing at all is worth doing badly."

The success and value of this conference were such that if it could be repeated two or three times in the next decade, preferably at some place like Douglas Lake, Put-in-Bay, or even at one of the universities where summer work in ecology is emphasized, the progress of ecological studies, and the unity and perhaps the dignity of the science would benefit. With the *American Midland Naturalist*, *Ecology* and *Ecological Monographs* available for printing the proceedings, it should be possible for such a series of informally arranged conferences to do much toward supplying a needed mutual understanding among ecologists and toward a closer and, of course, entirely voluntary integration of our research.

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TROUT STREAMS¹

At long last there is available a book on trout and trout waters that will appeal to a wide variety of persons, from fisheries specialists through sports fishermen to prospective wardens seeking a "cram manual" and even professors of terrestrial zoology in need of lecture material on aquatic forms. Dr. Needham is eminently qualified for authorship in this field. He has studied trout of both Atlantic and Pacific watersheds, having earlier been engaged with the "Biological Survey" of freshwater streams in New York

¹ Needham, Paul R. 1938. Trout streams, conditions that determine their productivity and suggestions for stream and lake management. x + 233 pp., 74 figs. Comstock Publishing Company, Ithaca, N. Y. \$3.00.

State and more recently on the California Trout Investigation. His experience in these diverse habitats affords breadth of perspective seldom available to a worker in this field and has tended to eliminate a provincial attitude. To this background he brings the zest of a fisherman, an appreciation of the pleasantries of the out-of-doors, a critical scientific appraisal of his own investigations as well as those of others, and finally a practical viewpoint as to things possible and impossible in the way of fish and habitat management.

The book opens with an account of the North American trout and salmon, including native, introduced and transplanted forms. Their physical characteristics and variations are set forth clearly, often in tabular form. Then follows discussion of the physical and chemical conditions of trout waters, of the animal inhabitants of trout streams and lakes, of the foods selected by trout, of the occurrence of food animals both ecologically and seasonally, of propagation, stocking and protection of trout and finally of stream and lake management.

The work contains an abundance of established factual material, including many heretofore unpublished data from investigations by the author and some from other workers in the field, while deficiencies in existing knowledge are often indicated. Practical directions are given for collecting specimens and data relating to trout, their food and their habitats, including descriptions of the necessary apparatus and record forms.

The author's vision of the "trout problem" under conditions and viewpoints existing in the United States is of a long-time program that will first obtain adequate technical knowledge of the subject and then make proper application of such knowledge. Apropos of planting fish he says (pp. 174-175): "All too often the hatcheryman's interest ends when the fish leave the hatchery. . . . In many cases the vicious result is a 'paper record' of huge numbers planted. . . . if they [the hatcherymen] were given more responsibility in seeing the fish they have raised properly planted, the result should be a higher survival to the angler's creel. . . . If a larger proportion of the angler's dollar were spent in developing a more efficient planting system it would undoubtedly give greater returns. . . . There is no good reason why public fishing waters in general cannot be so managed as to offer as fine sport as private waters, once the problem is understood and the cooperation of fishermen at large is obtained."

Throughout the volume an effort is made to replace qualitative information and speculation with quantitative data. The enormous variety in local conditions precludes absolute statements suited for general use in all trout waters.

A small amount of the text deals with current, sometimes transient, conditions in local waters. These materials serve in places as examples or to fortify a thesis and will probably be replaced in subsequent editions.

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THE CALIFORNIA WOODPECKER AND RITTER¹

"This is chiefly an amateur's book, by amateurs for amateurs," but despite its popularized style it raises some very fundamental questions. The author states that his purpose in making this study was "to increase my understanding of the California woodpecker and of myself . . . to bring into as clear a light as possible wherein we are alike and wherein we are different." To this end he has made an extensive study of the natural history of the California woodpecker (*Balanosphyra formicivora bairdi*) which is represented in the first and largest section of the book, and in the three sections which remain he compares the biological backgrounds of the bird and of himself and explores the philosophical implications.

The distribution, abundance, food habits, breeding habits, social habits, special habits and evidences of positive and negative adaptability are described in considerable detail in the first section. A good part of this material has been reviewed by Professor Ritter in a previous publication (1929. *Quart. Rev. Biol.* 4: 455-483).

The accounts of frequent cooperation in breeding of more than two birds, and of special adaptability and maladaptability are of interest. Communism was noted in the drilling of the nest hole, copulation, egg-laying and incubation, and feeding of the young. Storage holes are drilled to the size of the acorn, acorns of conveniently manageable size are taken most often, and soft-barked trees are the ones selected for storage in a mixed stand. On the other hand such useless objects as pebbles and date pits are sometimes stored, and abortive holes may be made from which the nuts can be readily removed by rodents. An instance is described in which over 62,000 nuts were knocked through the thin walls of an abandoned miner's house, and hollow trees may similarly be filled with nuts beyond the future reach of the birds. The writer stresses the limitations of his method in that the desirable continuity of observations and identification of individuals was not possible.

Part II compares birds and men—their fundamental similarity in the unique organization called life, their general homologies and specializations, comparative reproduction, ancestry, and physiological basis of size differences.

Part III, drawing evidence largely from comparative neurology and inspiration from C. J. Herrick, the neurologist, places special emphasis on the differences of most consequence, i.e. the superiority of man to bird in capacities for individual adjustment localized in his highly developed cerebral cortex, as compared to the evolutionary limits imposed upon birds by their specialization as flying machines. Birds, however, in those sensory and adaptive capacities whose centers lie in the old, subcortical brain, are superior to all

¹ Ritter, William Emerson. 1938. The California Woodpecker and I. A Study in Comparative Zoology. Univ. Calif. Press, Berkeley, California. xiii + 340 pp. Col. Frontis. \$3.50.

other vertebrates, including man. The cortical deficiency of birds is somehow correlated with their specialization for locomotion while the cortical superiority of primates is correlated with the development of arms and hands. The special advantages of man in the growth of language and tradition are not treated. In the chapter on adaptivity and maladaptivity in men and woodpeckers, no maladaptations are mentioned for man, curiously enough, as e.g. his often misdirected skill in mass destruction of his species and frequent unbalancing of his environment. There is a philosophical discussion of the nature of adaptation in accordance with the well-known holistic conceptions of the author (1919. *The Unity of the Organism*. 2 vls.).

Part IV summarizes the accomplishments towards the original purpose of the book. Some important gaps in the factual knowledge of the woodpecker are indicated which would require an experimental approach. Additional ideas developed in this section are the emotional and esthetic values of living and of curiosity, and the idea of responsibility according to capacity of the species.

The principle feature of the book is the comparison and evaluation in some detail of a bird and a mammal, top representatives in this case of two different lines of evolution. There is no absolute standard for judging biological success or efficiency. Within the broad limits of the problems of self-preservation and of group-perpetuation, to which the author seems to restrict the discussion, a number of quite objective criteria have been considered by various authorities which, for the purpose of quantitative treatment and evaluation, could be related to the total amount of energy transformed either at a given moment or during the entire history of a group. Such criteria are: numbers (as determined by the birth-death rate ratio), diversity (related to numbers through ecological valence and vagility), size, rate of activity, degree of control over the environment (number of energy chains indirectly controlled or influenced), and length of the period of activity.

All of these are touched upon more or less explicitly by Ritter who emphasizes what are probably the two most important: the capacity for rapid individual adjustment to a change in environment, and longevity of the race without narrowing or closing the channels for future evolution.

The book is interesting and easy to read. It reflects the author's broad and dynamic viewpoint of his subject, his enthusiasm for it, and his philosophical leanings. A large field is covered, although treatment of some topics is admittedly cursory. The book is permeated by the idea of the organism as a whole. There is an index and a bibliography and a number of illustrations including portraits of the California woodpecker and of Dr. Ritter.

NICHOLAS E. COLLIAS

EVOLUTION ¹

This collection of essays on evolution has been published in honor of Professor E. S. Goodrich. Although there is little continuity of style or subject matter between the essays written by the numerous authors, interesting facets of evolution are presented by capable authorities. The volume should be on the shelves of every student of modern development in the theory of evolution.

Poulton presents an interesting historical background through his long association with the leaders of evolutionary thought. He also argues that protective coloration and mimicry are proof of natural selection. Huxley gives a scholarly summary of the concept of sexual selection. Besides a useful classification of the grades of sexual adjustment and interaction, he shows that most of the facts are best explained through the action of intraspecific and interspecific selection, thus placing the sex adjustments on a par with many other adaptations resulting from the forces of natural selection. Ford, in his essay on "The Genetic Basis of Adaptation," indicates that selection acts through a balance of environmental factors, that convergence often is based upon different physiological and genetic mechanisms, and that parallel mutations do not satisfactorily explain mimicry.

In his discussion of "Embryology and Evolution," de Beer considers ontogeny in the light of evolutionary genetics. He draws the rather astonishing conclusion that, "while continuity of homologous structures implies affinity between organisms in phylogeny, it does not necessarily imply similarity of genetic factors or of ontogenetic processes in the production of homologous structures." It seems to the reviewer that de Beer loses sight of the fact that we are unaware of the existence of a genetic factor unless it has undergone mutation, so that our knowledge of the genetics of any single complex adaptive character probably rests upon an analysis of only a small percentage of the genes that are actually involved. Our knowledge of the thresholds of activity of the gene complex is also in its infancy.

Haldane discusses the nature of interspecific differences and concludes that species may differ in large numbers of genes while varieties often differ in respect of one or a few genes. Varieties may be regarded as incipient species. It is the opinion of the reviewer that the evidence points to the general applicability of this rule with the possible exception of certain chromosomal differences between many species of plants. The conclusion is not in accord with Goldschmidt's concept of the relationship between subspecies and species.

Richards gives a critical evaluation of taxonomic methods. Carr-Saunders discusses certain eugenic and disgenic tendencies in man. Elton, in an interesting essay on "Animal Numbers and Adaptation," gives a concise state-

¹ de Beer, G. R. (Editor). 1938. *Evolution*. 351 pp. *Oxford University Press*. \$5.00.

ment of the conclusions already published in his ecological books. Hardy, in an essay entitled, "Change and Choice: A Study in Pelagic Ecology," shows the relation between environment and vertical migration in plankton organisms. Such information establishes ecological position as a primary requisite of every organism beside the classical requisites of nutrition, defense and reproduction. Baker gives some interesting data and generalizations on "The Evolution of Breeding Seasons," thus bringing another aspect of periodism under consideration. Ecological position as a function of the nervous system is discussed by Young. Gatenby has an essay on "The Evolution of the Cytoplasmic Apparatus of the Cell."

Evolutionary tendencies and problems are also discussed in a series of essays by authorities on bacteria, protozoa, helminths, crustacea, echinoderms, fish and birds. Thus the details of evolutionary events known best through the exact work of the taxonomic specialists are joined with the work of the students of evolutionary principles. Both approaches would seem to be necessary for any balanced consideration of the complex mechanism of organic evolution.

ALFRED E. EMERSON

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ANIMAL ECOLOGY¹

"Pearse has thoroughly revised and enlarged his well-known book on Animal Ecology and has included a series of figures and photographs which add to the interest of the text. Seven new chapters have been added which include discussions of climate, evolution, chorology, succession, climaxes, rhythms, communities, competition, populations, teaching, ecological problems, and economic ecology. The bibliography is extensive and has been brought up to date.

In the opinion of the reviewer, Pearse's book published in 1926 gave a more comprehensive outline of the field of animal ecology than any other work. The revised edition is even better in this respect than the first edition. Many of the biases of other ecologists do not appear in the book nor have they interfered with a comprehensive interpretation of the field. Although the general viewpoint is broad, the book is more of an outline of the literature than a critical evaluation of ecological theory.

There is no doubt that this work will occupy a central position in the library of every student of animal ecology. It is particularly valuable as a concise reference book, but it will doubtless be used as a text in many courses on animal ecology.

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¹ Pearse, A. S. 1939. *Animal Ecology*. 2d edit. 642 pp. 133 figs. McGraw-Hill Book Co., New York and London. \$5.50. "

A LABORATORY GUIDE TO THE CLASSIFICATION AND ECOLOGY OF ANIMALS¹

This manual is a revision of earlier works by Allee and Shelford, but much new material has been added by Park together with valuable additions in the form of an introduction to ecology, field and laboratory exercises, keys to local animals of the Chicago area, as well as a revised key to the orders of animals. A glossary, bibliography and index are added. Several excellent original figures will help the student to visualize portions of the text.

The book has been built around the popular course in Ecology given at Northwestern University by Park. The subject matter is largely the outgrowth of field work in the Chicago region, but will prove of great value to ecologists in other parts of the United States. The exercises will serve as models for instructors in field zoology. Several of the exercises are quite original, such as that on cave animals of Kentucky. The reviewer intends to place this book in the hands of each student in his course in Field Zoology and recommends it enthusiastically to other teachers of Ecology.

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ANTS AND MEN¹

It is seldom that popular books written by non-professional biologists present more than half-baked interpretations of the more superficial aspects of the subject. This comparative study of ants and men has been written by a young chemist and the reviewer fully expected to find it full of anthropomorphisms if not gross errors of fact and theory. Instead he found a remarkably authoritative summary of the life and evolution of ants and mature comparisons with human society. Although courage is needed in making such comparisons, the author carefully guards himself from dogmatism or over-enthusiastic bias and makes a real contribution to the theory of society. His review of the levels of social coordination among the ants together with his discussion and interpretation of the phenomena of slavery, parasitism, commensalism, war and competition is scholarly. The book is extremely well written and deserves its selection by the Scientific Book Club. It is written for the layman and is immeasurably better in both fact and philosophy than the popular works of Maeterlinck on bees and termites.

The discussion of "mathematical, engineering, literary and artistic mutants" among men; the comparison of ant and human totalitarian states; and the parallelism of interspecific relations of ants and intraspecific relations of men are some of the weaker parts of the book from the standpoint of a biologist. If these analogues prove to be superficial in time, however, the author has not erred more than such distinguished myrmecologists as Forel and Wheeler.

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ALFRED E. EMERSON

¹ Park, O., W. C. Allee and V. E. Shelford. 1939. A Laboratory Introduction to Animal Ecology and Taxonomy. 272 pp. 17 pls. Univ. Chicago Press. \$2.00.

¹ Haskins, Caryl P. 1939. Of Ants and Men. vii + 244 pp. 15 pls. Prentice-Hall, Inc., New York. \$2.75.

BOOK NOTICES

Duncan, C. D. 1939. A contribution to the Biology of North American Vespine Wasps. *Stanford Univ. Publ. Biol. Sci.* 8 (1) : 1-272; 255 figs. Paper \$2.50, Cloth \$3.25. This is a comprehensive study on the morphology, generic taxonomy, and biology of the Vespinae. The biological portion deals with the life cycle metamorphosis, food relationships, and nest building activities of the wasps. The discussion of cannibalism, populations and nesting behavior is of particular interest to ecologists. The whole monograph is a worthy contribution to the study of social insects.

Davis, W. B. 1939. The Recent Mammals of Idaho. 400 pp. 33 figs.* 2 pls. *Caxton Printers, Caldwell, Idaho.* \$5.00. The ecology and taxonomy of Idaho mammals has been reviewed in this book. Many distributional maps are included with discussions of the state geography, floral provinces, distributional areas, distributional problems and notes on the various species. Keys for identification and brief descriptions of the Idaho species together with certain taxonomic revisions and a bibliography are incorporated.

Wheeler, W. M. 1939. Essays in Philosophical Biology (selected by G. H. Parker). 261 pp. 1 pl. *Harvard Univ. Press, Cambridge, Mass.* \$3.00. Because so many of Wheeler's gems of biological humor and philosophy were out of print, Dr. Parker brought together some of the best into this attractive book. The collection includes I. The Ant-colony as an Organism, II. Jean-Henri Fabre, III. On Instincts, IV. The Termitodoxa, or Biology and Society, V. The Organization of Research, VI. The Dry-rot of our Academic Biology, VII. Emergent Evolution and the Development of Societies, VIII. Carl Akeley's Early Work and Environment, IX. Present Tendencies in Biological Theory, X. Hopes in the Biological Sciences, XI. Some Attractions of the Field Studies of Ants, XII. Animal Societies. An excellent photograph of Wheeler, a picture of the tablet to his memory in the Museum of Comparative Zoology and an appreciation signed by I. J. Henderson, Thomas Barbour, F. M. Carpenter, and Hans Zinsser are included.

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NOTES AND COMMENT

A TEMPERATURE STUDY OF A WISCONSIN PEAT BOG¹

While recovering peat samples from more than a score of bogs in northern Wisconsin during August of 1938, a rather surprising temperature curve was noted. The temperature at the surface of the bog closely parallels the prevailing temperature of the air, but at progressively lower levels the temperatures drop sharply. This continues until near the bottom of the deposit a temperature is usually found that is several degrees warmer than that at levels slightly higher.

An attempt to find an explanation for such a temperature curve was made by a critical study of one peat deposit in Vilas County, Wisconsin. The bog in which the following observations were made is located in Section 26, Township 42 North, Range 7 East. It formed in a glacial kettle hole in a pitted outwash plain. The cover is *Chamaedaphne calyculata*. The deposit is oval in surface outline and is approximately 370 feet long and 135 feet wide. Eight borings were made with a Davis peat sampler at approximately fifty-foot intervals along the longer axis of the bog. Sand was found below the peat at all places. Two pits were dug to the water table in the sand plain at a distance of ten feet from each end of the bog. Station 1, the test pit in the sand at the west end of the deposit is in dense brush while Station 10, the sand test pit at the east end is in open woods. This may account for the difference in the temperature of those soils.

Immediately after withdrawing the peat sample from the bog a small Centigrade thermometer was partially inserted in the tube. It was left in place until the mercury had dropped to its lowest position and was read at the first indication of a rise. The following readings were obtained (table I):

TABLE I. *Temperatures in degrees Centigrade in a peat deposit-*

Stations										
Feet	1	2	3	4	5	6	7	8	9	10
0	16.6*	19	15.1	15.5	14	17.8	16.2	15.9	15.4	19.5*
1	15.0*	15.1*	14.0	15.7	15.7	16.4	16.5	16.6	15.0	16.5*
2	14.8*		12.0	14.4	14.7	14.9	14.7	15.5	13.4	16.0*
3			13.1*	12.4	13.0	12.8	12.8	12.7	11.5	
4				11.0	11.1	11.3	11.9	11.6	13.3*	
5				9.6	10.1	9.9	9.9	9.9		
6				12.0*	8.9	8.9	8.8	9.1		
7					8.0	8.4	8.2	8.8		
8					7.6	8.0	7.7	7.9		
9					7.5	7.6	7.5	9.4*		
10					7.7	7.4	7.2	7.8		
11					7.8	7.4	7.2	12.5*		
12					7.7	7.8	7.3			
13					11.2*	8.0†	8.1†			
14						7.5	7.2			
15						9.4*	7.3			
16							7.7			
17							8.3*			

* Sand.

† Peat less fibrous than above or below.

¹ From the Limnological Laboratory of the Wisconsin Geological and Natural History Survey. Report No. 90.

The explanation for the temperature curve in table I appears to lie in the fact that there is greater conductance of heat in sand than in peat. Also that fibrous peat is less of a conductor than the finely divided, so called, limnic peat. The fibrous types usually occur above the more homogeneous peat; the latter usually in direct contact with the sand foundation of the deposit.

It appears that the greater warmth of the lowest peat over that which is some distance from the top must be explained as being warmed from the sand below, since the sand shows higher temperatures than the peat. A study of table I shows that the sand about the bog (Stations 1 and 10) has a relatively high temperature and as one proceeds from the periphery of the bog to the deepest section (Station 7) there is a graded decline in the temperature of the sand. It appears that the heating of the sand is from the periphery of the deposit and not from the earth's interior. When the length and thickness of the peat deposit is drawn to scale upon paper, it becomes evident that the peat forms but a slight veneer over the sand plain. This may further demonstrate the possibility of the peripheral origin of the heat in the lower levels of the bog. Slow decomposition in the lowest levels of the bog may be suggested as the cause of such a temperature curve. Sufficient bacterial activity is doubtful since the humic acids, which are present, do not favor excessive bacterial growth.

Certain bog lakes have been observed that have similar temperature curves (Juday, Birge, and Meloche, p. 40; Welch, p. 441)² as the bog under discussion and further investigations of these may show a similar heating phenomena.

The writer wishes to thank Dr. Paul S. Conger and others who have helped at various times in the recovery of peat samples used in the above study.

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INFRA-RED PHOTOGRAPHY AS AN AID IN ECOLOGICAL SURVEYS¹

During experimental work leading to the development of infra-red-sensitive photographic materials, Dr. R. W. Wood, of Johns Hopkins University, discovered that various types of vegetation, all similarly colored, were by no means similar in their ability to reflect infra-red radiation.

Until recently, infra-red-sensitive photographic materials have not been available in sizes and speeds suitable for use by the average worker. Today, infra-red-sensitive roll film, cut film, and plates are obtainable "over the counter," and may be profitably employed, within their limitations, in ecological survey work.

Coloring of vegetation, as perceived by the unaided eye, is due largely to the presence of chlorophyll in the inner structure of the leaves. As all leaves contain chlorophyll relatively close to the surface, and covered by layers which are substantially transparent to most of the visible spectrum, the visually similar coloring of different types is not surprising; and the near-impossibility of differentiating these types by color or tone in visual observations or in most photographs taken on panchromatic films (which have a color sensitivity roughly approximating that of the human eye) can be readily understood.

The reflection of infra-red radiation by the leaf bears little relation to the perceived color, being largely a property of the epidermal layers, and of the cutin. The behavior

² Juday, C., E. A. Birge, and V. W. Meloche. 1935. The carbon dioxide and hydrogen ion content of the lake waters of northeastern Wisconsin. *Trans. Wis. Acad. Sci. Arts and Letts.* 29: 1-82.

Welch, Paul S. 1938. A limnological study of a retrograding bog lake. *Ecology* 19: 435-453.

¹The field work here described was supported by a grant from the Penrose Fund of the American Philosophical Society.

of these layers toward infra-red radiation varies considerably from one plant type to another; somewhat, in some cases, from one genus to another; and occasionally at different stages of growth or in different states of nutrition in the same genus and species.

Field tests, checked many times, show that grasses and certain cacti are the best reflectors of infra-red radiation, most of them having a greater infra-red reflecting power than newly-fallen snow. As a result, these plant types will appear as a brilliant white in a finished print from an infra-red negative (see figs. 1, 2, and 3).

Mature and drying grasses and unhealthy cacti are poorer reflectors of infra-red radiation, and appear in a finished print as a light gray tone (fig. 3, foreground).



FIG. 1. Phantom Valley, Grand County, Colorado. This photograph shows a longitudinal distance of seven miles, a transverse distance of three miles, and a vertical distance of 2800 feet, not including sky areas.

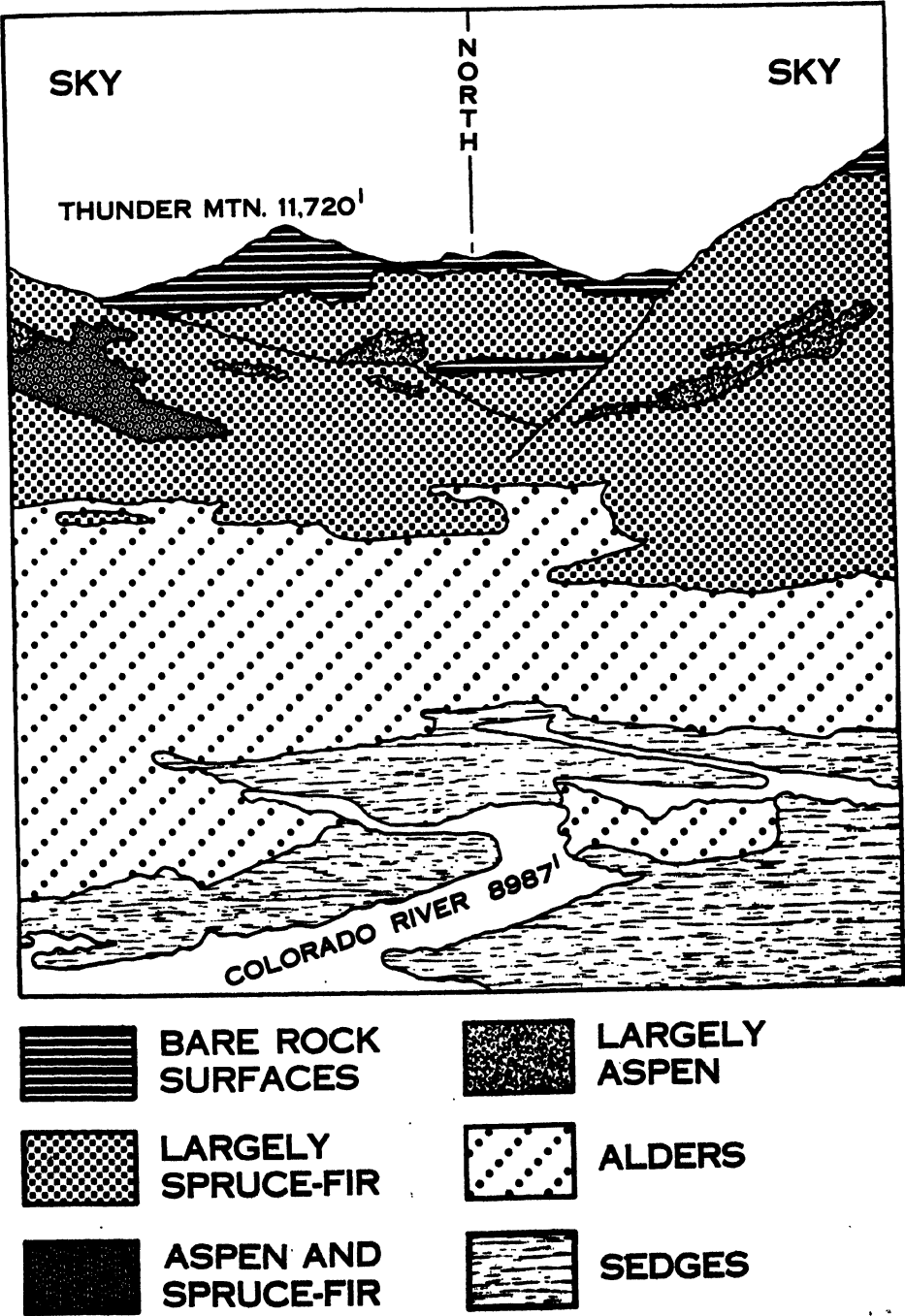


FIG. 2. Vegetation types in Phantom Valley, as determined from a study of figure 1 and as checked in the field.



FIG. 3. Infra-red photograph of the Stillwater Basin, Grand County, Colorado, showing the variations in tone of grasses (foreground) caused by soil and water differences. Note that the horses (in circle, lower left) have chosen the best pasture. The white area in the middle distance, just within the boundary of the spruce-fir forest, is the grass covered outwash fan of an ephemeral stream.

Deciduous vegetation, in general, is a good reflector of infra-red, and appears in a finished print as a light gray—almost white, but not as white as healthy grasses (figs. 1 and 2, *alders* and *aspens*; also in figure 3 note the lighter-colored aspen growth in old burned-over areas in the spruce-fir forest in the left distance, just below the skyline).

Evergreens, in general, are poor reflectors of infra-red, and appear in a finished print as a dark gray or black (figs. 1 and 2). It should be noted that young needles are fair reflectors of infra-red, and hence will appear lighter, in an infra-red photograph, than mature needles. For this reason, some of the trees in the spruce-fir forest of figure 1 have white-tipped limbs.

EQUIPMENT

Almost any reasonably good camera of relatively recent manufacture will function satisfactorily when used for infra-red work. The only requirements are that the camera be in perfect mechanical condition, and that infra-red-sensitive films or plates to fit it are available. The accompanying photographs were taken with a 3¼" by 4¼" Speed Graphic, equipped with an 8¾" Bausch and Lomb Tessar lens.

Lenses. Any reasonably good lens will give satisfactory results in infra-red photography. While many lenses are not fully corrected for use in this work, they will give clear sharp images if focussed visually, then stopped down to about F. 22 before the exposure is made. Figures 1 and 3 were exposed at F. 32 (8¾" lens), and at this aperture the lens-film-atmosphere combination has a revolving power of more than 800 lines per inch under normal weather conditions. The limiting factor, in almost every case, is the atmosphere, rather than either the lens or film.

Filters. The correct filter depends upon the sensitive material employed, and is usually specified by the manufacturer of the plate or film. In general, a light red filter, such as a Wratten A, is adequate to remove the unwanted blue and yellow light. Either gelatine filters mounted in glass, or glass filters must be used: unmounted gelatine filters upset definition: cellophane filters introduce unwanted polarization effects.

Tripod. A good husky tripod is almost essential in infra-red work. More photographs are "lost" because the camera moved during the exposure than from any other single cause. Any good rigid tripod will be satisfactory, but it *must* be rigid. In very rough country, a "tilt and pan" tripod head will be found useful.

Exposure meter. No good exposure meter for infra-red work is at present commercially available. Any good photoelectric exposure meter will be useful as an approximate guide, but correct exposures for various subjects and light conditions are best determined by means of "test shots."²

When infra-red photographs are used in connection with ecological surveys, it must be borne in mind that the camera is a tool, and that the photographs secured are a means to an end: not an end in themselves. Surveys made solely by photographic means are seldom of much value, but good photographs plus careful field work lead to a greatly increased accomplishment per day spent in the field.

Careful advance planning will do much to increase the effectiveness of field photographs, and to minimize the labor of taking them. Whenever possible, if an area is to be completely "covered," the photographic stations should be tentatively located in advance, with the aid of a topographic map. "Blind areas," such as the upper end of Phantom Valley in figure 1 (the part of the valley behind the shadowed cliff in right center), must be "covered" by taking additional photographs, sometimes a very laborious and expensive procedure. By careful planning, the stations can be so chosen that the number of "blind areas" is minimized.

² With Eastman Infra-Red Plates, type 1R-1, in combination with a Wratten A filter, a Weston speed of 3.2 gives satisfactory results in the Rocky Mountain and Great Basin regions. On the Atlantic seaboard, a slightly slower Weston speed gives better results, according to test exposures.

Whenever possible, a large part of the area included in one photograph should be studied in detail, after a print has been obtained. This will give the field worker an accurate key to the plant types present, and to the tones in the photograph representing them. Unless careful field checking is done, errors such as classifying a grove of cottonwoods as an aspen patch are likely to be made.

Several photographs of each scene, each exposed differently, are desirable to guard against exposure trouble. This is a safety measure, economically justified when the labor and cost of returning to the field for a "retake" is compared with the cost of the additional film used.

Development of infra-red plates and films *must* be done in *total darkness*. "Time and temperature" development is almost mandatory in this case. Any standard developer, properly used, will give good results. Special fine-grain development is not necessary unless enlargement of more than ten diameters is contemplated.³ No special attempt should be made to get extra contrast in the development, as infra-red photographs of outdoor subjects tend to be too contrasty. Additional contrast, if desired, is best obtained by printing on "hard" paper.

Manufacturer's instructions, supplied with the plates or films, are the best guide to darkroom procedure, and, if followed carefully, will almost invariably lead to successful results.

Because of the superlative infra-red photographs recently taken by Capt. A. W. Stevens and a few other superskilled and well-equipped photographic specialists, there is a common tendency to overestimate the potentialities of infra-red photography.

Field tests show that the useful range of the infra-red camera, in ecological work, is ordinarily not more than ten miles. In special cases, where only great changes in the vegetation need be detected, the useful range is somewhat greater. Timberlines, for example, on mountain ranges 50 miles from the camera, can be quite accurately located in infra-red photographs, but aspen patches known to exist in the spruce-fir forests on the flanks of these ranges cannot be detected in the pictures.

The probable accuracy of classifications made from photographs decreases as the distance of the subject from the camera increases, as a result not only of the decreasing angle subtended by the subject as the camera is moved away from it, but of the degradation of contrast resulting from scattered light in the air.

In figure 1, the aspen patch on the near side of Thunder Mtn., about six miles from the camera, is darker in tone than the nearer aspen patches, and is of the same tone as the barren rock areas above timberline. This is a result of contrast degradation. That this area is an aspen patch, and not slide-rock, was determined by inspecting the plate under a low-power microscope, and checked by inspection of a photograph of the same scene taken on panchromatic film. In the panchromatic photograph the suspected area was of a different tone than the nearby slide-rock. Unless tree structure could be determined by microscopic examination of the plate, or the presence of vegetation shown by comparison of the infra-red view with a photograph taken by different colored light, or a description of the area found in the field notes, classification would not have been possible without an additional trip to the field.

While, in most cases, plants in a single picture that are the same tone belong in the same classification, confusion may occur where two environments are included in one photograph. This is clearly shown in figure 3, where different foreground tones show healthy grasses (white) on well-watered areas of deposition, and drying grasses (gray) on areas being eroded. In the upper right, just below the skyline, is an area of the same

³ Developers such as Eastman D-76 and Eastman Ultra Fine Grain, and similar developers of other manufacture, give consistently good results with infra-red-sensitive materials. These developers give satisfactorily small grain size in correctly-exposed plates, are not critical as to either time or temperature, and have a long life.

tone as the healthy grass. This could be classified, on the basis of tone, as a well-watered area of deposition, which is obviously wrong. The actual condition, on this 11,000-foot peneplain, is one of erosion, with adequate moisture to support vegetation—a condition in marked contrast to the semi-arid erosion occurring in the basin in the foreground.

In avoiding errors of classification, a little common sense, coupled with much care in the field, is more valuable than several volumes of rules and formulae.

CONCLUSIONS

Infra-red photographs are a valuable aid in ecological field work, but they are by no means a substitute for that work.

Each geographic area is an individual problem, and techniques entirely satisfactory in the intermontane basins of Colorado, for example, may not work on the flatlands of Kansas, or in the arboreal deserts of Sonora.

Photographic techniques are useful only when they have been tested carefully in the areas concerned, and the worker is fully aware of what they will do, *and what they will not do*.

The writer is indebted to Mr. J. E. Gunderson, of the Eastman Kodak Co., for technical photographic information; to Dr. Gordon Alexander, of the University of Colorado, for suggestions in connection with this paper; and to Mr. Gordon Snow, of Boulder, Colo., for competent assistance in the field.

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POPULATION STUDIES IN COLONIES OF *POLISTES* WASPS; WITH REMARKS ON THE CASTES

Studies of population in the social *Polistes* wasps can indeed be misleading, if one is not absolutely certain as to the number of foundress queens in each colony. Since one cannot distinguish queens from workers—and this is true for at least the four species found in this region—it is necessary to be on hand during early stages of colony-founding so that the foundress queen or queens may be given distinguishing marks before the workers appear. During 1938, I was able to mark queens and observe the population of two colonies of the species *pallipes* and of one each of *annularis* and *variatus*.

The first of these was a nest of *pallipes* built on the ceiling of an open-faced shed in my yard. On April 24, I found one queen on the nest of ten shallow cells; a few days later four additional small cells were constructed. This foundation was all that was made by the queen and she spent her time thereafter in enlarging these and in feeding the growing larvae. More cells were made by the workers later in the season. Forty-five days after the first eggs were deposited (June 4), the first larva completed its feeding and spun a cap over the cell, preparatory to pupating. A week later (June 12) three additional cells were similarly covered. On June 30, the first two adults emerged from capped cells, having spent eighteen and twenty-six days each in the pupal stage, making a grand total of seventy days, more or less, from the time of deposition of the egg to the birth of the adult. Additional workers emerged from the cells from time to time and the first male emerged on August 11. From September 10 to 20, the wasps at various times abandoned the nest. A count of the cells at the end of the season gave the following figures: nine shallow empty cups around the outer edge of the nest (too small to have given forth adults) and forty-one large cells from which adults had emerged. In addition, ten of the original cells were used twice for young, thus making the total population of the colony (the offspring of one queen) fifty-one adults. By

examining the amount of hardened excrement in a cell, one may tell whether or not it had been used one or more times for young. The larva, hanging head downward, discharges, just before pupating, the accumulated contents of the alimentary tract and plasters it, presumably by movements of the body, against the ceiling. There it soon becomes a hard, gritty mass.

A second *pallipes* nest was studied at Diecke, Mo. The lone queen on the nest was marked on June 10 and observed occasionally during the summer. On September 25, I found the nest had been abandoned; a study of the cells later revealed twenty small cells around the periphery (from which nothing had hatched or possibly could have hatched) and sixty-seven large cells from which adults had emerged; there were also sixteen cells in the center (original cells) which were used twice. This nest, therefore, had a total population (the offspring of one queen) of eighty-three adults.

A nest of *P. annularis* at Diecke, Mo., with two queens and no workers (none of the cells were large enough to have given forth workers) was first observed on June 4. The two queens were marked and it was noted that there were thirty-two large cells, each with egg or larva and also eleven sealed cells. A week later, on June 12, I found only one queen on the nest; the other had abandoned it. The number of the cells, forty-three, remained the same; no additional ones had been built. There were now five adults on the nest and each of the cells from which they had emerged now contained an egg. These first five workers were puny and undersized; the same condition was also noted for the first brood of workers of *Vespa maculata* (Ann. Ent. Soc. Amer., 22: 659-675. 1929) and again for the first brood of *Polistes variatus* which is described on a later page. This dwarfed condition is not, however, constant for all colonies of *Polistes* wasps, for in other nests of both *pallipes* and *annularis*, I found the first brood of workers to be of normal size. I presume that when food is scarce in early spring, or when the foundress-queen is sluggish the undernourished larvae metamorphose into dwarfed adults.

In examining the nest on July 4 and again on August 14, I found many workers on the nest, but no males at all. On September 25, I found the nest abandoned; a count of the cells showed seventy-three small peripheral cells (a few with larvae), ninety large cells that had given forth adult wasps; there were also twenty-two of these (original cells) that had harbored two larvae each, thus making a total population of 112, the product of two queens, one of which had not served full time.

I have elsewhere referred to the fact that the cells of *Polistes* are often used more than once. This statement gives the impression, I believe, that all of the cells are used more than one time. Upon closer study of the problem, I find that for the most part only the original cells, those that are first to be vacated in the season, are so used. The later cells, those made by the workers, are vacated too late in the season (at least in this climate) to be of any use for a second brood, and if so used the young seldom mature before winter. In warmer climates the social wasps doubtless get a much larger tenancy-turnover per cell than they do in the temperature zone.

At Diecke, Mo., a nest of *variatus* was studied. The one queen on the nest probably commenced nest-building very early in the spring, for on June 4, it had four undersized workers and also, what was more surprising, a male among them. This is an extremely early date for male *Polistes* to emerge. The following are normal records of male emergence. The first male emerged from each of three *pallipes* nests in St. Louis County in 1938 on August 7, 10 and 11. In one nest of *rubrigenosis* and in two of *annularis* brought from Arcadia, Mo., six males of the former species and several each of the latter emerged from August 6 to 10, but I do not know if these were the very first males to hatch from these nests. Obviously, July 25 is too early for normal emergence of males, but on August 30, at Pacific, Mo., I examined five *pallipes* nests and one *variatus* and found males on all of them.

On September 25 most of the members of the Diecke *variatus* colony had disbanded but there were still a dozen workers and males clinging to the nest. I removed the nest for study, however, and found fifty-six small peripheral cells (too small to have harbored adults), a dozen of which had half-grown larvae destined to perish with the on-coming cold. There were 185 cells from which adults had emerged in addition to twelve original cells which were used twice for brood, thus making a total population of 197 adults. This is a surprisingly large population (the work of one queen) but one may see its plausibility in cases where the queen gets an exceptionally early start in the spring and in turn has an early brood of workers to relieve her of all duties but that of egg-laying.

DISCUSSION

In investigating a problem of this kind one soon learns that merely a count of the cells in *Polistes* nests does not give a true picture of colony-population. In such studies, not only must one know the number of foundress-queens to each nest, but one must also know the number of cells that have been occupied more than one time by growing larvae as well as the number of valueless unfinished cells that may be empty at the end of summer or may at most contain young that are destined to perish with the approach of winter. This study, however, falls short in two respects of giving a complete picture of colony-population in these wasps. The first of these is that no consideration is given of the ratio of the number of wasps that are born to the number of adults that remain on the nest. Wasps get lost, suffer from vicissitudes of environment, as well as fall prey to enemies. What this proportion is can only be discovered by marking each adult as it emerges, and then observing it, from time to time, to the end of its days. Even if time and patience allowed this, one would have no proof that those which failed to return were not lost to predaceous enemies because of the conspicuousness of the bright paint marks. The second lack is that no consideration can be given to the number of individuals in each caste of the colony. It will be remembered that colonies of social wasps are supposed to be composed of queens, workers, and males, but an accurate count of two of the three castes is not possible, since, as already stated, there exist no distinguishing characteristics between queen and worker. Until we are able to find morphological differences between the two, or until we actually discover that queens and workers are one and the same, no progress can be made in this aspect of population study. The suspicion that workers and queens may be the same caste has caused me to form some speculative thoughts on the subject, which I wish to discuss in the following paragraphs.

CASTES OF *Polistes* WASPS

We have for a long time taken for granted the existence of three castes in *Polistes* wasps although proof, experimental or observational, is not at hand to support this contention. It is true that foundress wasps begin nest-building in the spring of each year but may it not be that these are merely the "workers" of the past autumn that have become inseminated and have survived the winter in a state of hibernation? It seems to me that doubt as to the existence of three castes is quite permissible since there are no morphological and no psychological differences between queens and workers. This lack of psychological difference may easily be seen in studies of queenless (orphan) colonies where workers, which have never seen the foundress of the nest, behave like the queen in all activities of nest-fabrication and brood-care.¹ Carefully planned experiments may prove the correctness of the assumption that foundress-queens are merely those late-emerging workers of yesteryear that have not had an opportunity to exhaust their vitality

¹ See articles in *Jour. Comparative Psychology* 10: 267-286, 1930; 27: 259-269, 1939 and *Ent. News* 40: 226-232, 256-259, 1929.

in heavy labor and have been among those which have appeared on the scene sufficiently late to meet the young males and mate with them. This untapped vitality as well as insemination may have given them the impetus to hibernate as well as to found new colonies.

If it could be experimentally proven that the *polistes* colony consists only of males and females, with the latter serving two rôles, we would have a condition connecting the two well-known extremes in the reproduction proclivities in the family Vespidae. I refer on the one hand to the solitary Eumenid wasps, where only the usual two sexes exist, and on the other to the highly organized social members of the genera *Vespa* and *Vespula*, where there is to be found as substantial a morphological difference between queen and worker as in any of the most highly organized colonies of social bees. *Polistes* would then take her place midway between these two extremes by virtue of the fact that as an ordinary female she may and can at times assume the rôle of queen.

This idea, if one may speculate a bit farther, would relieve us of the task of explaining by what process the queen manipulates her spermatheca in order to deposit "at will" fertile or infertile eggs; we could then assume and probably experimentally prove that hibernating females, because of their having mated, lay only fertilized eggs which produce workers and that unmated workers, because of their virginity, deposit only infertile eggs which hatch into males. Each "caste," therefore, would be powerless to deposit any other kind of eggs. One may also see the probability of old "workers," because of their advanced age and worn condition, being no match to younger rivals when the males appear at the end of the season.

The remarks herein expressed may, to say the least, seem unusual but there are a few well known facts that lend support to this theme; for example, Dr. Wheeler states² (p. 120) that in certain species of social bees and wasps that live under unfavorable conditions, such as in the arctic regions, the worker caste is completely or almost completely suppressed. Further, there is additional evidence to support the two-sex idea in *Polistes* by what is known of the behavior of a very near relative in another part of the world. Dr. Wheeler² (p. 88) in quoting von Ihering and Rabaud says that the worker caste in *Belongaster* in Africa is "either absent or very feebly developed and constitutes only a small percentage of the female personnel of the colony"; again on page 77, "the emerging females are all like the mother in possessing well developed ovaries and being capable of fecundation . . . all the females of the colony are physiologically equal and even such differences in stature as they may exhibit have no relation to fertility."

Returning for the moment to an earlier remark about the queen and worker each depositing one kind of egg, I find that Verlaine (*Biol. Abstracts* 6: 620, 1932) furnishes experimental data on bees, bumble-bees, wasps, and ants in support of this view.

To conclude, then, it seems that one may legitimately suspect that worker *Polistes* wasps, like their African cousins, are capable of fecundation at the end of the season when males appear; also that it may be possible for them to perpetuate themselves as do the *Belongaster* wasps in Africa with however this difference; in temperate regions the advent of hibernation occurs between fertilization and colony-founding, while in the tropics the fertilized workers go off and found new colonies at once.

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TOURIST ANTS

There are a number of species of ants, particularly tropical species, which have become widely distributed yet there are astonishingly few records of ants actually found on ships. This does not indicate, of course, that few ants travel on the ships themselves but rather that seldom are they collected, identified, and the records published. The records include:

² *Social Life among the Insects*, 1923.

- Ponera punctatissima* Rog. S. S. Chenab between Trinidad and Cuba (Myers, '34).
Monomorium pharaonis L. Ship from West Africa (Forel, '01); S. S. Korona, British Guiana (Wheeler, '16); Ship on the Rio Negro and R. Branco and S. S. Bahia; on the Rio Amazon, Brazil (Bequaert, '26); S. S. Chenab between Trinidad and Cuba (Myers, '34); S. S. Inca in the Patagonian Canal at Aysén, Chile (Goetsch and Menozzi, '35).
Monomorium destructor (Jerd.). S. S. Colombia, between San Francisco and Baltimore via the Panama Canal (Clarke, '22).
Paratrechina longicornis Latr. S. S. Silesia (Wheeler, '08); S. S. Korona, British Guiana (Wheeler, '16); S. S. Chenab between Trinidad and Cuba (Myers, '34).
Campanotus (Myrmecopis) sericeiventris Guer., ssp. *rex* Forel. Ship from Panama (Wheeler, '31).

There are more records of ants found in soil about plants and in merchandise which have been intercepted by plant quarantine officers at the docks or later found established in places such as greenhouses and botanical gardens. Still another manner of introduction is indicated by finding in September, 1933, in luggage in Cambridge, Mass., several days after my return from Cuba, workers of the tropical *Monomorium destructor*. The voyage was made on the S. S. Veragua but ants were not seen on the ship. It is much more probable that the ants were acquired in my hotel in Havana, where they were abundant.

Forel (see Donisthorpe, '27) lists the following as the eleven cosmopolitan ants introduced by shipping: *Odontomachus haematoda* L.; *Pheidole megacephala* F.; *Monomorium pharaonis* L.; *Monomorium floricola* (Jerd.); *Monomorium destructor* (Jerd.); *Solenopsis geminata* F.; *Tetramorium guineense* F.; *Tetramorium simillimum* F. Smith; *Tapinoma melanocephalum* F.; *Paratrechina longicornis* Latr.; *Paratrechina vividula* Nyl.

These are such inveterate globe trotters as to be found on nearly every island in the warmer regions of the world and on every continent except the Antarctic. Their method of dispersal usually is not exactly known but generally they are assumed to be carried "in commerce" from port to port. These cosmopolites consequently are found first in seaports and they may or may not be able to invade the country. *M. pharaonis* has penetrated even to the central part of North America where it was abundant last winter in Grand Forks, N. D. It has evidently been established in offices and other buildings in Grand Forks for a number of years. Temperatures here in the winter of -20° to -30° Fahr. are not uncommon and -42° was recorded in 1936. According to Dr. A. E. Emerson *M. pharaonis* became a pest in the Michael Reese Hospital, Chicago, Ill., from 1929 to 1933, and I was shown specimens at the University of Minnesota from Rochester and Minneapolis, Minn. Factors governing the establishment of these cosmopolites in alien lands include climate, available food, etc., but above all an adaptability which seems to be specific, and in *Monomorium*, generic. As a rule it is the small to minute species which are most successful but *Odontomachus haematoda* is a large and conspicuous exception. Sometimes, as in such small islands as Bermuda and some of the Lesser Antilles, the introduced ants drive out most of the indigenous ant fauna. An introduced ant may even drive out an earlier migrant as *Iridomyrmex humilis* Mayr, a South American ant, drove out *Pheidole megacephala* from Madeira (Wheeler, '06).

During various voyages in the American Tropics, I have been interested in ants which were found to be fellow passengers, even cabin mates, and the following are these records:

1. *Neoponera (N.)* sp. near *foetida*—S. S. Apure, 22.I.35, Orinoco River, Venezuela. Neotropical species.

2. *Odontomachus haematoda* L.—S. S. Apure, 17.II.35, Orinoco River, Venezuela. Cosmopolitan species.
3. *Pheidole fallax jelskii* Mayr.—S. S. Apure, 22.I.35, Orinoco River, Venezuela. Neotropical species.
4. *Crematogaster (Orthocrema) brevispinosa* Mayr.—S. S. Apure, 22.I.35, Orinoco River, Venezuela. Neotropical species.
5. *Crematogaster* sp. (not *brevispinosa*)—S. S. Apure, 22.I.35, Orinoco River, Venezuela. Neotropical species.
6. *Monomorium floricola* (Jerdon)—S. S. Bisra, 13.VI.36, Essequibo River, British Guiana. Cosmopolitan species.
7. *Monomorium pharaonis* (L.)—S. S. Lady Drake, XI.34, between Boston and Trinidad; S. S. Lady Hawkins, 9.VIII.35, between Trinidad and British Guiana; S. S. Van Rensselaer, 5.VI.36, between Trinidad and British Guiana; S. S. Oranje Nassau, X.36, between British Guiana and New York; S. S. Cerigo, between Buenaventura, Colombia and Panama, 11.VIII.38. Also a United Fruit Co. steamship, X.38, between New Orleans and Honduras, in cabin (D. E. Farringer). Cosmopolitan species.
8. *Solenopsis geminata* (Fabr.)—S. S. Apure, 17.II.35, Orinoco River, Venezuela. Cosmopolitan species.
9. *Tetramorium guineense* (Fabr.)—S. S. Apure, 17.II.35, Orinoco River, Venezuela. Cosmopolitan species.
10. *Tetramorium simillimum* (F. Smith)—S. S. Apure, 22.I.35, Orinoco River, Venezuela. Cosmopolitan species.
11. *Cryptocerus (Hypocryptocerus)* sp.—S. S. Apure, 22.I.35, Orinoco River, Venezuela. Neotropical species.
12. *Cryptocerus (Cyathomyrmex) varians* F. Smith—S. S. Apure, 22.I.35, Orinoco River, Venezuela. Neotropical species.
13. *Tapinoma melanocephalum* (Fabr.)—S. S. Apure, 22.I.35, Orinoco River, Venezuela. S. S. Bisra, 13.VI.36, Essequibo River, British Guiana. S. S. Ancon, 3.VI.38, between New York and Haiti. Cosmopolitan species.
14. *Asteca* sp.—S. S. Apure, 22.I.35, Orinoco River, Venezuela. Neotropical species.
15. *Paratrechina (P.) longicornis* Latr.—S. S. Apure, 22.I.35, 17.II.35, Orinoco River, Venezuela. S. S. Bisra, 13.VI.36, Essequibo River, British Guiana. Cosmopolitan species.
16. *Paratrechina (Nylanderia) vividula* Nyl.—S. S. Apure, 22.I.35, Orinoco River, Venezuela. Cosmopolitan species.

Seven of these sixteen species are not cosmopolitan ants but are confined to the Neotropical Region. Their presence, all on the S. S. Apure, is accounted for below. The S. S. Apure also carried seven of the eleven cosmopolitan species and two additional species (*Monomorium pharaonis* and *Pheidole megacephala*) may well have been carried but not seen on the two passages.

Of the well-known cosmopolitan ants, only two, *Monomorium destructor* and *Pheidole megacephala*, were not found on these voyages and I have mentioned *M. destructor* as found in luggage upon returning from Cuba.

The S. S. Apure is a stern paddle-wheel steamer plying between Port-of-Spain, Trinidad, B. W. I. and Ciudad Bolivar on the Orinoco River, Venezuela. Stops are made at several points along the river and in the Delta for fuel, which is wood gathered by Indians from the practically unbroken rain forest. Of the ants recorded from this ship *Solenopsis geminata*, *Tetramorium guineense*, *T. simillimum*, *Tapinoma melanocephalum* and *Paratrechina longicornis* appeared to be regular inhabitants and were found in my cabin as well as in various parts of the ship. The other ants were taken mostly near the boilers on the floor or on the wood stacked nearby. They undoubtedly were

acquired with the wood, in which most could have been nesting. The *Neoponera* stung me painfully, and, with the *Odontomachus*, were avoided by the barefooted and bare-legged stokers. Additional inhabitants or travellers on the ship included the ubiquitous cockroaches, Trichoptera, Coleoptera, especially Rhynchota, Lepidoptera (moths), several species of Tabanidae and hordes of mosquitoes as we passed through the Delta.

The S. S. Bisra is another stern paddle-wheel steamer operating from Georgetown, British Guiana along the coast to the mouth of the Essequibo River, largest river of the colony, and up the river to Bartica, at the junction with the combined Mazaruni-Cuyuni rivers. The *Tapinoma* and *Paratrechina* workers were abundant, taking particles of food from the vicinity of the dining table, and generally over-running the ship. One *Monomorium* worker was taken from my plate at the dining table, another from my arm on the deck.

The S. S. Lady Drake and Lady Hawkins operate between Halifax, Boston, Bermuda, the British Lesser Antilles, Trinidad and British Guiana. The S. S. Rensselaer and Oranje Nassau operate between North European ports, Madeira, from Surinam to Puerto Cabello on the Venezuelan coast, Curaçao, Haiti and New York. The S. S. Cerigo operates between Ecuador, Pacific ports of Colombia, Panama (Canal Zone) and occasionally to Atlantic ports of Colombia. *Monomorium pharaonis* workers were present in variable numbers in the cabins of these ships. Commonly, when they were abundant, workers would form long files up and over the washbasin to the faucet where they drank water. On the Cerigo they even explored the berths and were suspected of stinging. An unusual insect on this latter ship was a fruit-fly (Trypetidae) which probably emerged from fruit on the ship. A large dragon-fly (Odonata: Anisoptera) was also seen but flew off towards the Colombian mainland, probably 25-50 miles away.

I have been told by officers of some ships that the fumigation the ships occasionally receive keeps the ants down only a voyage or two, when they may again become conspicuous. The fumigation may kill only the workers foraging about; the queen or queens, well hidden in crevices, may escape and in a few weeks produce another brood.

These ants recorded above came on the ship in various ways, probably in cargo or passenger luggage. Some may emulate passengers and walk on over the gangplank, as they could easily at the Orinoco stops of the S. S. Apure, where the simple plank was laid down on the sandy beach with the dense forest but a few feet away. Ants of some cosmopolitan species are commonly found in warehouses on the docks. If cargo stands long enough it would be simple for colonies to become established in it and later carried into the ship. All of the cosmopolitan species and many others show remarkable versatility in nesting habits. I have personally found ant colonies nesting in walking sticks, teapots, between the leaves of books, bureau drawers, containers of all kinds and, in general, almost any place which is small and largely covered. Worker ants scurry about on anything left even momentarily on the docks but they are not particularly significant since they do not reproduce themselves.

SUMMARY

Sixteen species of ants were taken on ships in the American Tropics. Of the sixteen, nine are well known ants which are widely distributed in the tropical and warm temperate regions of the world. Two other kinds not found on these ships with the above nine constitute the eleven cosmopolitan species of ants; one of these two was found in luggage in the U. S. upon return from Cuba.

Monomorium pharaonis was taken on six ships. This species and *Paratrechina longicornis* are probably the most common ship ants and may be expected on any vessels visiting ports in warm regions.

A single ship carried seven of the eleven species of cosmopolitan ants; five of these appeared to be regular inhabitants.

Worker ants are regularly carried into ships in cargo and passenger luggage. Since they do not reproduce themselves they are a nuisance only during their lifetime. But when a queen is carried in cargo, a colony may become established on the ship or deposited with the cargo in an alien port. Factors governing the establishment of ants in alien lands include climate, available food, etc., but, above all, an adaptability which seems to be specific, and, in *Monomorium*, generic.

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DENSITY CURRENTS IN NORRIS RESERVOIR

There are two principal ways to determine the existence of subsurface currents: (1) Direct measurements of these currents, and (2) by making various determinations of the chemical and physical character of the different strata of water. The former method was used by Evans¹ in a study of "The Undertow" in ponds and lakes. The through Lake Constance (Bodensee). Observations now in progress on Lake Mead and other reservoirs in the southwestern United States employ both methods, although at first the indirect method alone was used. Routine limnological observations on Norris Reservoir, Norris, Tennessee, suggested the existence of density currents. Their existence was suggested by the vertical distribution of dissolved oxygen (D.O.), turbidity, methyl orange alkalinity (M.O. Alk.), and at times by pH and nitrite nitrogen. Factors that favor the development of density currents in Norris Reservoir are due in part to conditions within the reservoir, for instance, differences in temperature at different depths, and in part to the character of the incoming water; temperature below that of the surface of the reservoir, high turbidity, low salinity associated with high turbidity and low temperature, etc. The operation of the reservoir—withdrawal of water at the dam well below the upper limit of the hypolimnion, the volume of discharge and the

¹ Evans, O. F. 1938. The Undertow. *Science* 87: 279-281.

second was used by Auerbach and Ritze² in a study of the flow of the River Rhine

² Auerbach, Max and Max Ritze. 1937. Der Lauf des Rheinwassers durch den Bodensee. *Archiv f. Hydrobiologie* 32.

volume of incoming water—determines the degree of permanency of these currents. In 1937, such a stratum of water retained its identity for a distance of between 40 and 50 miles. The same thing holds for 1938, only the lines of demarcation between the different strata are less definite in 1938. This is accounted for by a much larger flow of water from the tributaries at critical periods. Monish and Keulegan³ have shown experimentally that with a given density gradient the relative velocity of the density current plays a leading rôle in the permanency of the identity of the strata of water involved. If the velocity is too low and the different strata are miscible then diffusion at their interphase will destroy their identity. If, on the other hand, under these conditions, the

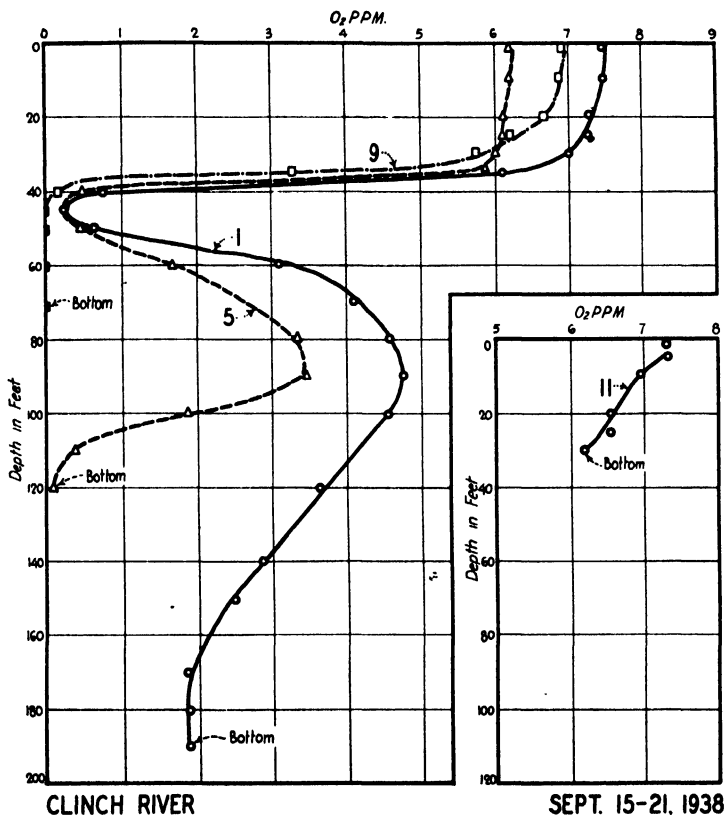


FIG. 1. Shows vertical distribution of dissolved oxygen at four different stations on Clinch River Sector. The numbers on the curves denote stations.

velocity exceeds a critical value, turbulence will cause a mixing of the water of the different strata.

Figure 1 illustrates the vertical distribution of D.O. at four stations on the Clinch River sector of Norris Reservoir in 1937. Curve No. 1 shows conditions one-quarter mile above the dam (Sept. 21). Curve No. 5 is for a point 19 miles above No. 1 (Sept. 20). Curve No. 9 shows conditions approximately 22 miles above No. 5 (Sept. 15), and curve No. 11 represents conditions about 12 miles above No. 9 (Sept. 15). These

³ Monish, B. H. and G. H. Keulegan. 1930. Appendix E., Report of the Inter-divisional Committee on Density Currents. April 30. *Bur. of Standards*.

locations differ only in the distance above the dam and the total depth of the water (these depths mark the lower extremity of the curve in Figures 1 to 3).

We note (Fig. 1) that curves of D.O. No. 1 and No. 5 indicate a minimum at 45' and then a second maximum at 90'. Curve No. 9 also reaches a minimum at 45', but shows no increase below this depth. Curve No. 11 shows only a decrease of a little more than 1 p.p.m between surface and bottom. It may be mentioned here that the stratification with respect to temperature was normal and that vertical changes in temperature occurred at the same level at all stations, that is, a curve showing the temperature at any given depth for all stations was a straight line. The low D.O. at from 40 to 50' was always

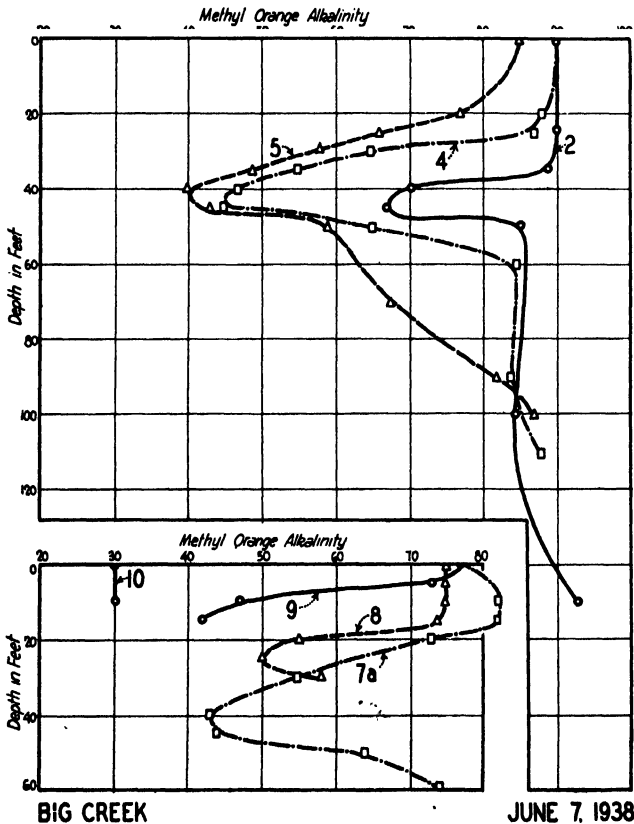


FIG. 2. Shows vertical distribution of methyl orange alkalinity in p.p.m. in Big Creek Sector. The numbers on the curves denote stations:

within the region of the thermocline. The explanation for this atypical D.O. pattern is as follows, and these remarks are based on observation and experiments. During the summer months, the incoming water is relatively warm and well aerated, but because of the silt complex⁴ carried by it, the oxygen demand of this water is relatively high. Laboratory tests made in 1938 show that toward the head of the reservoir, where the depth of the water is around 50', the demand is sufficient to use up all the oxygen the water contains at all levels in from less than 7 to less than 14 days. It is in this depth,

⁴ Whitney, L. V. 1937. *Science* 85: 224-225, has shown that the strata of high turbidity contain more bacteria than the less turbid strata.

where the water first comes to rest, and it is here that bottom stagnation begins. Much of the silt load is also deposited here. The oxygen demand further down where the depth is around 130' is much less (no blanks after 14 days). The result is the formation of a pool of stagnant water along the bottom near the head of the reservoir, while the water further down still has a high D.O. content at all depths. Under the influence of the discharge at the dam, the water moves toward the dam, but it moves at its density level. The deeper water further down is much colder and heavier (temperature differences as much as 38° F. between surface and 140' have been observed in the deeper sections of the reservoir). When this warm stagnant water meets the much colder and hence heavier water, it flows over the surface of the latter. This stagnant water, however, is colder than the surface water and thus it does not mix with the latter. The temperature range of the intrusion sheet of stagnant water in 1937 was always within the limits of the temperature range of stagnant water at the head of the reservoir.

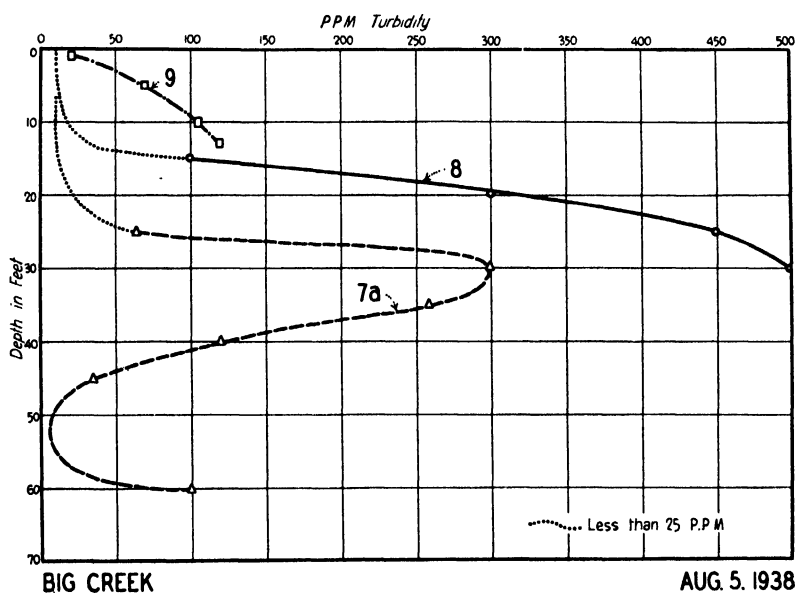


FIG. 3. Shows vertical distribution of turbidity in p.p.m. in Big Creek Sector. The numbers on the curves denote stations. Numbers and location as in figure 2.

The existence of a density current in the Big Creek Sector of the reservoir on June 6, 1938, was traced by measuring the methyl orange alkalinity (Fig. 2). The fact that this water of low alkalinity travelled below the surface was due to a lower temperature of the incoming water (period of cold rains) and silt. The increase due to silt and temperature more than compensated for the loss in density due to reduced salinity. The curves (Fig. 2) are numbered in decreasing order from the head of the reservoir No. 10 to No. 2, about 8 miles below No. 10. These numbers correspond to stations. Curve No. 10 reflects the low alkalinity of the incoming water. Curve No. 9 shows the minimum alkalinity at the bottom, but all the other curves show the minimum at 40 to 45'. The reduced thickness of this stratum of water at No. 2 is due to an increase in the cross-section of the reservoir. It was noted at the time that at No. 2 and No. 4, the stratum of low alkalinity was turbid while the water above and below was clear. At the remaining stations the turbidity began to show in this layer, but was not confined to it. It persisted with increasing intensity to the bottom. This suggests that a density current due to

silt is less stable than one due to difference in salinity or temperature. Incidentally the conditions with respect to the water of low alkalinity are very similar to those found by Auerbach and Ritze.²

Figure 3 illustrates the formation of a density current due to silt. Curve No. 9 shows turbidities higher than 25 p.p.m. with maximum at bottom (Jackson Turbidimetre) from surface to bottom. Curve No. 8 (this station is 0.5 mile below No. 9) shows turbidity less than 25 p.p.m. at a depth of ten feet, but the maximum is still at the bottom. Curve 7a (point 1.5 miles below No. 8) shows turbidity less than 25 to a depth of 20 feet; a maximum of 300 at 30 feet, with less than 50 p.p.m. at 45 feet (the apparent increase at 60' may have been caused by the sampler coming in contact with the bottom). Density currents due to silt have been traced in the Clinch River Sector from the point of origin to a distance of 22 miles below this point.

In conclusion, it may be repeated that no actual measurements of currents have been made, but that the measurement of chemical and physical factors bear evidence for their existence. At least density currents, if present, help materially in the interpretation of conditions in Norris Reservoir.

This investigation is still in progress and it is hoped that a complete report with more detailed data can be published eventually.⁵

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LAND HOLDINGS OF NORTH AMERICAN UNIVERSITIES WITH PARTICULAR REFERENCE TO GRASSLAND¹

Recent years have seen a development in ecology, forestry, wildlife management, etc., which has called for the use of land for instruction and for the research of professors, instructors and graduate students in the leading institutions of learning. Harvard, Yale, Cornell, Duke, Johns Hopkins (a small area) and Chicago among the endowed institutions have come into possession of forest lands for these purposes. Likewise the state institutions such as the Universities of Michigan, Wisconsin, Illinois, Missouri, Minnesota, Indiana, Georgia and North Carolina, Ohio State University and many others have forest holdings.

In spite of all the disaster that recent years have shown to agriculture and industry in the Plains States, only five institutions hold any *grassland* for scientific research and instruction. The institutions in the blacksoil prairie area at the eastern edge do not have any. There is serious need for continuous observation of grassland, for the restoration of perennial grasses to hold the soil against wind erosion, and for restoration of grasses on plowed lands. To make the best use of grassland much knowledge must be acquired bearing on the relations of grasses to soil, rodents, grasshoppers, etc. Grassland also has advantages for general biological study due to the general visibility and convenient arrangement of its vegetation features.

Still the greatest centers of grassland study, such as the Universities of Arizona, Texas, Oklahoma, Kansas, Nebraska, Iowa, Illinois and Saskatchewan and likewise the agricultural colleges of the same states and provinces, are without lands for *research and instruction*. Of the five institutions owning grassland only one (Colorado Agricultural

⁵ Published by permission of the Authority.

¹ Prepared for the National Research Council Committee on the Ecology of Grasslands of North America, V. E. Shelford, Chairman, by The Ecological Society of America's Committee for the Study of Plant and Animal Communities, R. E. Yeatter, Secretary.

College) grants the Ph.D. degree. Three of the others grant Masters' degrees only, and the Oklahoma College for Women gives no advanced work.

The most valuable lands are those within 20 minutes of the campus and available to the teaching investigator and advanced student in a vacant 2 hour period. Next in value are lands within two hours or less from the campus so that instruction or investigations may be carried on with half days free. At the Universities of Nebraska, Oklahoma, Arizona, Texas and Saskatchewan, and at North Dakota Agricultural College, lands leased or held by other public organizations have been used. However, disaster has overtaken a large grassland research project involving the research of a half dozen men on a proposed long time study due to a change of policy in the land-holding body. Others have suffered from cancellation of leases, etc. This has involved essentially all the four or five grassland projects that have been set up by institutions of learning.

This information was brought out by a questionnaire sent to 150 of the leading colleges and universities of the 600 or more listed by the U. S. Bureau of Education. The results of the questionnaire are presented below.

Of the approximately fifty (uncultivated) land owning institutions included in the returns, 38 report that the areas are used for both class work and research, 7 report areas used for research only, 5 for class work only.

As to details of use, 43 report use for plant ecology; 40 for animal ecology; 40 for game management; 24 for forestry; 22 for reforestation; 16 for animal population cycles; 6 for insect pest prediction; 7 for erosion control; 6 for restoration of grasses; and 6 for grazing studies. Uses for plant and animal problems are essentially equal, each being about 100. Grazing studies are considered to be combined plant and animal problems.

As to management (more areas than institutions are reported), 20 report areas managed by a faculty committee, 18 (mainly professional schools) by a Director or Dean, 6 by a department, 6 by the Superintendent of Buildings and Grounds or Business Manager, and 3 each by the President or a special caretaker.

The lands are classified primarily on the basis of the length of time required to reach them. While there had been some doubt as to the limitations of the three categories set up, this was cleared very nicely in working over the questionnaire.

1. *Lands at Hand.* A great many institutions have tracts of land which may be reached in not more than 20 minutes from the campus. These were put under the category of "Lands at Hand." A 20-minute trip to an area permits a one-hour demonstration or lecture in the field in a two-hour period. Areas within 20 minutes of the campus are therefore especially valuable.

2. *Nearby Lands.* This group includes lands within a half to two hours of the campus. The nearer ones are available for half-day studies and the more distant ones for all-day studies.

3. *Distant Lands.* "Distant Lands" are $2\frac{1}{2}$ to 12 or more hours from the classrooms and laboratories. The more distant of these are available only for summer study. The list below indicates these lands arranged on the basis suggested. Several institutions known to have lands have not yet responded to the questionnaire. Some of these are Harvard, Cornell, the University of North Carolina and Kansas State Teachers College.

A provisional list of the land holdings is as follows:

N = Natural vegetation, more or less modified; S = Second growth; * = Added on basis of outside information.

LANDS AT HAND

Grassland

Colorado State College, Fort Collins, Colorado. 1,000 A. Short grass; foothills. *N*.
 *Kansas State Teachers College, Hayes, Kansas. Large area. Plains grassland. *N*.
 Montana, University of, Missoula, Montana. 100 A. Mixed grass. *N*.
 North Dakota Agric. Col., Fargo, North Dakota. 30 A. Mixed grass. *N*.
 Oklahoma College for Women, Chickasha, Oklahoma. 30 A. Grazed grassland. *N*.
 Washington State College, Pullman, Washington. 5 A. Bunch grass. *N*.

Northern Coniferous Forest

Alberta, University of, Edmonton, Alberta. 4 A. Aspen, white spruce. *N S*.

Pacific Coast Coniferous Forest

British Columbia, University of, Vancouver, British Columbia. 235 A. 2nd growth coniferous forest. *S*.
 Washington, University of, Seattle, Washington. 15 A. 2nd growth; ravines. *S*.

Mountain Coniferous Forest

Colorado, University of, Boulder, Colorado. 80 A. Aspen and lodge pole pine. *N*.
 Colorado State College, Fort Collins, Colorado. 16,000 A. Forest. *N S*.
 Montana, University of, Missoula, Montana. 430 A. Pine, Douglas fir, larch. *N*.

Deciduous Forest (Climax Area)

Augustana College, Rock Island, Illinois. 2 A. Oak hickory forest in ravines. *N S*.
 Bowdoin College, Brunswick, Maine. 500 A. Scrub pine and hardwoods. *N S*.
 Carleton College, Northfield, Minnesota. 350 A. Half natural, half uncultivated. *N S*.
 Carthage College, Carthage, Illinois. 9 A. Deciduous ravines, etc. *N*. Farm land—natural reforestation.
 Clark University, Worcester, Massachusetts. 10 A. Deciduous forest. *N S*.
 Connecticut Agricultural College, Storrs, Connecticut. 650 A. 2nd growth hardwoods and some conifers. *S*.
 *Cornell University, Ithaca, New York. Not reporting.
 Dartmouth College, Hanover, New Hampshire. 30 A. Sphagnum bog—spruce and white pine. *N*.
 Duke University, Durham, North Carolina. 4,523 A. 2nd growth pine and hardwoods. *S*.
 Florida, University of, Gainesville, Florida. 100 A. Semi-evergreen forest and swamp.
 Georgia, University of, Athens, Georgia. 1,000 A. Piedmont forest. *S*.
 Johns Hopkins University, Baltimore, Maryland. 15 A. Deciduous forest. *N*.
 Illinois, University of, Urbana, Illinois. 58 A. Deciduous climax and late subclimax. *N*.
 Maryland, University of, College Park, Maryland. 460 A. Sedge to white pine. *N S*.
 Massachusetts Agricultural College, Amherst, Massachusetts. 60 A. Mixed conifers and hardwood. Farmland. *N S*.
 Michigan State College, Lansing, Michigan. 204 A. Marsh, swamp hardwood, sugar maple, red cedar. *N S*.
 Michigan, University of, Ann Arbor, Michigan. 120 A. Hardwoods; swamp and lake. *N S*.
 New Hampshire, University of, Durham, New Hampshire. 75 A. "Old growth." *N*.
 *North Carolina, University of, Chapel Hill, North Carolina. Not reporting.
 Ohio State University, Columbus, Ohio. 50 A. Semi-mature hardwood forest. *S*.

- South Carolina, University of, Columbia, South Carolina. 7 A. Semi-mature hardwood forest. *S.* Conifers, hardwoods, herbaceous plants, planting going on. One tract (4½ A.) is to be botanical garden for native S. C. trees, shrubs, and wild plants.
- Sweet Briar College, Sweet Briar, Virginia. 50 A. Virginia woodland. *N S.*
- Tennessee, University of, Knoxville, Tennessee. 605 A. Wooded area, 2nd growth. *N S.*
- Western Reserve University, Cleveland, Ohio. 100 A. Beech-maple, etc., semi-natural. *N S.*
- Wisconsin, University of, Madison, Wisconsin. 800 A. Marsh, old fields, oak hickory. *N S.*
- Yale University, New Haven, Connecticut. 200 A. 2nd growth oak hickory and swamp hardwoods. *S.*

Institutions not granting Advanced Degrees

- Northern Illinois State Teachers College, DeKalb, Illinois. 30 A. Woods and grass. *N S.*
- Rosary College, River Forest, Illinois, 15A. Semi-natural. *N S.*
- Southern Illinois State Normal Univer., Carbondale, Illinois. 5 A. Flood plain; forest. *S.*
- Western Illinois State Teachers College, Macomb, Illinois. 25 A. Heavy woods, 2nd growth and grass. *N S.*

Chaparral and Woodland

- California, University of, Berkeley, California. 55 A. Chaparral; woodland. *N S.*
- Texas, University of, Austin, Texas. 500 A. Woodland and some grass. *N.*
- Colorado State College, Fort Collins, Colorado. 280 A. Chaparral. *N.*

NEARBY LANDS

Grassland

- Texas Agricultural and Mechanical College, College Station, Texas. Several A. Grass and brush, pasture-land; some post oak. *N S.*

Coniferous Forest

- Montana, University of, Missoula, Montana. 26,000 A. Conifers and some grass. *N S.*
- Utah State Agricultural College, Logan, Utah. 640 A. Montane forest, aspens. *N.*
- Colorado State College, Fort Collins, Colorado. 1600 A. Forest and grassland. *N S.*

Deciduous Forest

- Buffalo, University of, Buffalo, New York. 65 A. Tamarack swamp. *N.*
- Cincinnati, University of, Cincinnati, Ohio. 68 A. Woodland. *N S.*
- Duke University, Durham, North Carolina. 417 A. Pine and hardwoods. *S.*
- Florida, University of, Gainesville, Florida. 600 A. Pine, flatwoods. *N.*
- Georgia, University of, Athens, Georgia. 1,200 A. Piedmont forest. *N S.*
- *Harvard University, Cambridge, Massachusetts. 2000 A. Hardwoods and conifers. *N S.*
- Massachusetts Agricultural College, Amherst, Massachusetts. 755 A. Conifers and hardwoods. *N S.*
- Missouri, University of, Columbia, Missouri. 2,220 A. Deciduous 2nd growth. *S.* Leased 50 yrs.

- Michigan, University of, Ann Arbor, Michigan. 1,280 A. 2nd growth hardwood and pine. S.
 New Hampshire, University of, Durham, New Hampshire. 177 A. Deciduous woods and swamps. N S.
 Yale University, New Haven, Connecticut. 7,500 A. Hardwood and pine. N S.

DISTANT LANDS

Grassland

- Colorado State College, Fort Collins, Colorado. 6,400 A. Grass, etc.
 Iowa, State University of, Iowa City, Iowa. 25 A. Prairie at biological station.
 Texas, University of, Austin, Texas. Upwards of 2,000,000 A. Not available for scientific work.

Northern Coniferous Forest

- Bowdoin College, Brunswick, Maine. 650 A. White spruce and fir.

Coniferous Forest

- Montana, University of, Missoula, Montana. 288 A. Yellow pine and Douglas fir.
 Washington, University of, Seattle, Washington. 2,000 A. 2nd growth conifers.

Deciduous Forest

- Chicago, University of, Chicago, Illinois. 188 A. Oak, maple, linden, oak-hickory.
 Dartmouth College Hanover, New Hampshire.
 Kentucky, University of, Lexington, Kentucky. 15,000 A. 2nd growth. S.
 Michigan State College, Lansing, Michigan. 400 A. Hardwoods and swamp. N S.
 Michigan, University of, Ann Arbor, Michigan. Hardwood and conifers. N S.
 Missouri, University of, Columbia, Missouri. 40,000 A. Oak hickory. N. S.
 New Hampshire, University of, Durham, New Hampshire. 400 A. Forest, 2nd growth, etc. S.
 Ohio State University, Columbus, Ohio. 4,340 A. 2nd growth hardwoods and white pine. S.
 Yale University, New Haven, Connecticut. 1,500 A. 2nd growth white pine. S.

Southern Coniferous Forest

- Louisiana State University, Baton Rouge, Louisiana. 1,600 A. Pine.

The following reported possession of lands, the character of which is not clear: Butler University, University of Kansas, and the University of South Dakota.

The following reported land available by cooperative agreement with other biological agencies: The Universities of Arizona, Buffalo, California, Colorado, Delaware, Florida, Georgia, Illinois, Maine, Missouri, Nevada, Oklahoma, Tennessee, Washington; also the State Agricultural Colleges of Connecticut, Michigan, Montana, North Dakota; and in addition, Duke University, Washington University (St. Louis). Of these, the Universities of Arizona, Delaware, Maine, Nevada, Oklahoma, and Washington University (St. Louis) do not own natural or uncultivated lands. Also 15 other institutions have no such land owned or available. This list includes several of the best known institutions of high standing. It is, however, recognized that all institutions, especially the endowed ones, do not need to teach or do research in the subjects involved.

• V. E. SHELFORD AND R. E. YEATTER.

VEGETATION ON SCORIA AND CLAY BUTTES IN WESTERN NORTH DAKOTA

In his recent note Judd¹ has briefly outlined what he calls the course of plant succession on the "scoria" buttes of the badlands area of western North Dakota. In his discussion he seems to have included vegetation types that frequently occur in the immediate vicinity of scoria buttes but which are very doubtfully associated with scoria butte succession. He has pointed out, referring to Kellogg,² that the soil is highly alkaline and hence "only those plants that are alkaline tolerant can gain an early foothold and ecize." The most common pioneer species he finds to be *Artemisia longifolia* Nutt., *Artemisia dracunculoides* Pursh, *Atriplex hastata* L., *Chrysothamnus* sp., *Eriogonum multiceps* Nees, and *Salicornia herbacea* L.

While these species are found commonly on buttes in the badlands area, it seems well to point out that they are not necessarily found on "scoria" buttes. In tracing the course of plant succession on buttes in the badlands of western North Dakota it should be recognized that there are at least two distinct types of buttes in this area, and very probably several other varieties. There are "scoria" buttes, though pure scoria buttes are relatively few in number. Some buttes are entirely clay and shale, the clay butte being probably the most common. Less frequently buttes composed largely of soft sandstone occur.

Scoria is composed of shale, sandstone, and limestone, and was produced by the baking and fusing of material overlying burning lignite beds. The buttes composed solely of scoria are not very widely distributed in the area but good examples may be found in the vicinity of Ranger, North Dakota, where the eroded and rounded scoria tops support an isolated stand of western yellow pine, *Pinus ponderosa*. More frequently the scoria butte is actually a clay butte capped with a layer of scoria, this material being more resistant to erosion than the softer clay. Clay buttes not capped with scoria are also common, being generally composed of alternate, vari-colored, layers of clay, shale, sandstone, and lignite, with occasional limestone layers and concretionary rocks. Petrified wood occurs frequently in some of the clay and shale layers.

Pioneer stages as well as later stages in the development of the vegetation are different on these different types of buttes and the successional changes, because of the great heterogeneity of conditions that prevail even within restricted areas, are extremely complicated. Neither scoria nor clay buttes represent typical developments of the solonetz or alkali soil complex. Although alkali areas are frequent in small depressions on the clay buttes, and may be found occasionally on the scoria buttes.

The steep sides of the clay buttes, where the angle of slope is 60° or more, usually are not vegetated except for occasional scattered plants. In general, the vegetation that is found on the steep slopes of the clay buttes is a community of *Artemisia tridentata* Nutt., *Chrysothamnus graveolens* (Nutt.) Greene, and *Sarcobatus vermiculatus* (Hook.) Torr. *Eriogonum multiceps* Nees is frequently associated with this vegetation type, as well as *Atriplex confertifolia* (Torr.) S. Wats., *A. nuttallii* S. Wats., *A. hastata* L. and others. *Artemisia longifolia* also occurs frequently, as indicated by Judd, but is not necessarily a characteristic feature of the vegetation.

The grasses that appear most commonly associated with this clay-butte type of vegetation are *Agropyron spicatum* (Pursh) Scribn. and Smith and *Distichlis stricta* (Torr.) Rydb., the latter in the more alkaline spots associated with *Suaeda depressa* (Pursh) S. Wats.

¹ Judd, B. I. 1939. Plant succession on scoria buttes of western North Dakota. *Ecology* 20: 335-336.

² Kellogg, C. E. 1934. Morphology and genesis of the solonetz soils of Western North Dakota. *Soil Sci.* 38: 483-501.

A typical clay butte, representative of many similar buttes, with steep sides and flat top is found about 1.5 miles north of the Pyramid Range Laboratory in the badlands area. This butte is 60 to 80 feet high, 1000 or more feet long and 50 to 60 feet wide on top. On the steep slopes of the sides of the butte there is scarcely any vegetation. Occasional plants of *Artemisia tridentata*, *Artemisia longifolia*, and *Pachylophus caespitosus* (Nutt.) Raim., were observed. However, where small gulleys had formed, or in otherwise favored areas such as the nearly level ridge below an outcropping of lignite, *Artemisia tridentata* and *Chrysothamnus graveolens* were abundant. In such areas *Gutierrezia sarothrac* (Pursh) Britton and Rusby, *Eurotia lanata* (Pursh) Moq., *Atriplex nuttallii*, *Eriogonum multiceps*, *Musineon divaricatum* (Pursh) Coult. & Rose, *Gogswellia foeniculacea* (Nutt.) Coult. & Rose, *Phlox hoodii* Richardson, and *Pachylophus caespitosus* frequently occurred. *Agropyron spicatum* was present in scattered clumps.

The top of the butte, which was nearly level, supported a denser cover of vegetation. Grasses were more abundant and a greater number of species was present. *Agropyron spicatum* was frequent to abundant among the shrubs, which included *Artemisia tridentata*, *Chrysothamnus graveolens*, *Gutierrezia sarothrac*, *Eurotia lanata*, and *Atriplex nuttallii*. Other forb species such as *Eriogonum multiceps*, *Musineon divaricatum*, *Iva axillaris*, Pursh, *Phlox hoodii*, *Mertensia lanceolata* (Pursh) DC., *Allium textile* Nels. & Macbr., and *Opuntia polyacantha* Haw. were scarce to infrequent. *Bouteloua gracilis* (H.B.K.) Lag. and *Carex filifolia* Nutt. were also present in considerable abundance, and in certain areas these species with *Agropyron spicatum* formed a fairly dense ground cover. *Poa secunda* Presl. was associated with these species but was relatively less abundant.

The east end of the butte slopes at an angle of approximately 45°, a gentler slope than that which occurs on the other sides of the butte. On this slope in addition to the species previously mentioned one small patch of *Juniperus horizontalis* Moench. was found. There were also a few scattered bushes of *Symphoricarpos occidentalis* Hook. and *Rhus trilobata* Nutt. Additional species included *Oxytropis lambertii* Pursh, *Oroncarya glomerata* (Pursh) Greene, and *Achillea lanulosa* Nutt. *Agropyron spicatum* was the principal grass.

Other buttes examined near this one had *Atriplex confertifolia* and *Sarcobatus vermiculatus* associated frequently with the *Artemisia-Chrysothamnus* type of vegetation. The occurrence of this type on the small ridges below outcroppings of lignite veins is typical of these buttes. The vegetation thus developed is distinctive and striking when it occurs on the otherwise nearly barren sides of a clay butte.

On the tops of scoria knolls and on pure scoria buttes, however, the pioneer species are considerably different from those on the clay buttes. *Artemisia tridentata* rarely occurs and *Chrysothamnus graveolens* is occasionally present but is much less abundant on these slopes. The typical vegetation associated with the scoria butte might be characterized as the *Mentzelia decapetala-Juniperus horizontalis* type. These two species are frequently associated together on the scoria slopes where the scoria fragments have disintegrated but little and there has been scarcely any soil development, and on the tops of the scoria buttes. While *Juniperus horizontalis* often occurs on the clay slopes also, *Mentzelia decapetala* (Pursh) Urban & Gilg is found there much less frequently. With these species, shrubs such as *Rhus trilobata*, *Symphoricarpos occidentalis*, *Ghrysobotrya odorata* (Wendl.) Rydb., *Dasiphora fruticosa* (L.) Rydb., *Prunus virginiana* L., *Shepherdia argentea* Nutt., and *Prunus pumila* L. frequently occur. The principal grasses associated with this earlier stage are *Agropyron spicatum* and *Muhlenbergia cuspidata* (Torr.) Rydb. *Calamovilfa longifolia* (Hook.) Scribn., as well as others, are also occasionally present and *Carex filifolia*, *C. eleocharis* Bailey, and *C. pennsylvanica* Lam. are often present in lesser abundance.

A small scoria-topped butte about 2.5 miles N. W. of the Pyramid Park Range Laboratory was selected as being essentially typical of the buttes of this type in the badlands area. The average slope of the sides of the butte was estimated at about 55°.

The slope below, of course, became more gradual, while on top the surface was nearly level, rounding gently toward the edges. On the top of the butte, which was not over 10 to 15 per cent vegetated, *Agropyron spicatum* and *Muhlenbergia cuspidata* occurred in scattered clumps. There were a few stalks of *Calamovilfa longifolia* in isolated areas, and here and there appeared tufts of *Carex filifolia*. *Mentzelia decapetala* was abundant and prominent. Scattered patches of *Juniperus horizontalis* in good condition extended over the edge of the top and on down the sides for some distance. *Rhus trilobata*, *Dasiphora fruticosa*, *Artemisia longifolia*, and *Gutierrezia sarothrae*, were the principal additional woody species. *Penstemon* spp., especially *P. angustifolius* Pursh, *P. eriantherus* Pursh, *P. nitidus* Dougl., and *P. gracilis* Nutt. were frequent.

Meriolix serrulata (Nutt.) Walp. was scarce, as were *Petalostemon purpureus* (Vent.) Rydb., *Eriogonum multiceps*, *E. flavum*, *Lesquerella spatulata* Rydb., *L. alpina* (Nutt.) S. Wats., *Senecio columbianus* Greene, *Chrysopsis villosa* (Pursh) Nutt., *Paronychia sessiliflora* Nutt., and *Cheirinia aspera* (Nutt.) Rydb.

On the sloping sides, which were covered with pieces of loose scoria varying in size from less than 1 inch to more than 3 inches in diameter, essentially the same species were found. Additional species include a few scattered bushes of *Shepherdia argentea*, *Yucca glauca* Nutt., *Xylophacos missouriensis* (Nutt.) Rydb., *Psoraleidium argophyllum* (Pursh) Rydb., and *Artemisia cana* Pursh. The steeper parts of the slope were from 3 to 5 per cent vegetated. On the lower and less steep parts of the scoria slopes, *Agropyron spicatum*, *Muhlenbergia cuspidata*, and *Carex filifolia* became more abundant while *Andropogon scoparius* Michx. and *Bouteloua curtipendula* (Michx.) Torr. appeared in the association. The forbs were fewer in number on the lower slopes. As the slope became less steep toward the base and the clay material underlying the scoria assumed more importance, the character of the vegetation changed. *Bouteloua gracilis* became more abundant and the larger forbs disappeared. At the base of the slope *B. gracilis* occurred as an almost pure stand. Other scoria buttes examined in the area showed similar vegetation.

These two examples serve to illustrate earlier stages in the development of the vegetation on clay and scoria buttes. As the forces of wind and water erode and round off the tops of the buttes, and the slopes of the sides become more gradual, the grasses increase in prominence and the shrubby species tend to decrease in number and abundance, while the vegetation cover becomes more dense.

However, it should be pointed out that a rounded clay or scoria hill can no longer qualify as a butte, and any successional changes in vegetation occurring on such formations are entirely different from changes occurring on scoria or clay buttes. An outline of the successional stages in the development of vegetation in the badlands area of North Dakota as a whole is not being attempted in this brief note. Hanson and Whitman³ have pointed out that the classification of vegetation in the badlands of western North Dakota is difficult because of the great heterogeneity due to variations in topography, soil conditions, wind and water erosion, water penetration, accumulations of saline salts, and the influence of biotic factors. The determination of the course of plant succession in this area requires long-continued investigations on areas especially reserved for this purpose. The authors at present do not feel competent to outline the successional development of vegetation in this area, although they have been conducting investigations there for 5 and 8 years, respectively.

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³ Hanson, H. C. and Whitman, W. 1938. Characteristics of major grassland types in western North Dakota. *Ecol. Monog.* 8: 57-114.

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TEMPERATURE TOLERANCE AND RATES OF DEVELOPMENT IN THE EGGS OF AMPHIBIA¹

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Although the effect of temperature on the rate of embryonic growth in Amphibia was known before the turn of the last century, it remained for Lillie and Knowlton ('97) to supply the first quantitative data on the subject. They found that as the temperature was increased above the lowest at which eggs of *Ambystoma tigrinum* or *Rana pipiens* can develop, the time necessary to reach a given morphological stage becomes progressively less, until a temperature is reached above which normal development does not occur. It was also recognized that the time-temperature curve resembles those "measuring the rapidity of known chemical processes at different temperatures." In view of the work to be presented, it is of interest that they found the temperature tolerance of eggs to be correlated with environmental conditions. The eggs of species breeding early in the year when the water was cold, could tolerate a lower temperature than could those of forms breeding later in the spring. This paper of Lillie and Knowlton was followed by the masterly investigations of Hertwig in 1898, and others such as those of Galloway ('00), King ('03), Chambers ('08), Krogh ('14), Dempster ('33), Atlas ('35), and Knight ('38).

The present investigations are concerned with a comparison of the effects of temperature on the embryos of different amphibians. The temperature tolerance and rates of development, over a wide range of temperatures have been determined in four species of frogs. A comparison of developmental rate among four species of salamanders and between two toads has been made. Correlations between temperature tolerance and rates of development on one hand, and breeding habits and geographic distribution on the other, have led to certain conclusions regarding adaptation to environmental temperature

¹ It is a pleasure to acknowledge my indebtedness to Professor Barth who has directed these investigations, and to Professors Pollister and Barth for allowing me to use their data on rate of development in *Rana catesbeiana*. These investigations were aided in part by a grant in Chemical Embryology from the Rockefeller Foundation administered by Professor Barth.

conditions in these forms. A preliminary notice of these experiments has appeared (Moore, '38).

The Anuran genus *Rana* is represented by six species in New England and eastern Canada, namely: *R. sylvatica* Le Conte (in eastern Canada replaced by *R. s. cantabrigensis* Baird, according to Trapido and Clausen, '38), *R. pipiens* Schreber, *R. palustris* Le Conte, *R. clamitans* Latreille, *R. catesbeiana* Shaw, and *R. septentrionalis* Baird. The genus *Bufo* is represented by *B. americanus* Holbrook, and *B. fowleri* Hinckley, and the urodele genus *Ambystoma* by *A. tigrinum* (Green), *A. opacum* (Gravenhorst), *A. jeffersonianum* (Green), and *A. maculatum* (Shaw). These species differ in their geographic distribution and time of laying, with correlated differences in environmental temperatures to which the eggs are subjected. They form excellent material for studying adaptation to temperature differences. Data have been collected on all the above mentioned species with the exception of *R. septentrionalis*.

METHODS

The discovery that the ovaries of mature frogs can be stimulated to release their eggs by injecting the anterior lobe of the pituitary gland (Wolf, '29; Rugh, '34), has simplified the securing of eggs in early stages for temperature analysis. There is little difficulty in collecting eggs of *R. sylvatica* before first cleavage, as they are deposited when the water is cold and development slow, but this becomes increasingly difficult in the cases of species breeding later. It is with the latter that the pituitary technique has been most helpful. No differences have been detected between freshly collected eggs and those secured by injections. *R. sylvatica*, *R. pipiens*, and *R. palustris* collected in the autumn, produce eggs that give over 90 per cent fertilization and normal development when injected with *R. pipiens* pituitary glands. *R. clamitans* has not been injected in the autumn, but such treatment is successful in securing eggs in the spring before the normal breeding season.

The general procedure for frogs (*Ambystoma* and *Bufo* eggs were collected under natural conditions) was to fertilize the eggs artificially, and allow the jelly to swell. The egg mass was then cut into groups containing from 1 to 10 eggs, and several of these groups placed in finger bowls with 0.1 Amphibian Ringer's solution. Shortly before the onset of first cleavage, these bowls were placed at the desired temperatures. The eggs were examined at subsequent times, and the temperature of the 0.1 Ringer's and the stage of development recorded. Temperature control was by means of water-baths with mercury thermo-regulators, incubators, cold rooms, and refrigerators. Temperature measurements are in degrees centigrade.

The stages of development defined by Pollister for *R. sylvatica* (Pollister and Moore, '37) have been employed for all frogs (*Rana*) and toads (*Bufo*). Harrison's unpublished stages for *Ambystoma punctatum* have been used for all members of this genus.

The observations on rate of development are arranged in tables and plotted graphically. Thus Table I gives the time at which eggs of *Rana sylvatica* were observed in different stages at a variety of temperatures. When two figures are given they represent the earliest and latest hours at which eggs were observed in a particular stage. Thus at $15.3 \pm 0.3^\circ$ they are in stage 14 by 54 hours after first cleavage (stage 3). At 60 hours they are still in stage 14. Sometime between 60 and 63 hours they enter stage 15 but no observations have been made during that interval. The data in the $15.3 \pm 0.3^\circ$ column are composed of observations on eggs from two different females. One experiment was begun March 21, 1936, and the temperature was $15.4 \pm 0.2^\circ$. The second experiment was begun March 19, 1938, and the temperature was $15.1 \pm 0.1^\circ$. The number of females used in compiling the data in each column is indicated under "experiments" in the tables.

The graphs (Figs. 1-4) are constructed to simplify comparisons of the effect of temperature on rate of development. The data from one temperature are plotted as a straight line by varying the intervals between stages on the abscissa. Using this straight line as a base the data from other temperatures are then plotted. It is easier to compare the results at different temperatures when the base line is straight and the intervals on the abscissa varied, than when the latter are made uniform with a resulting irregular curve.

EXPERIMENTS

Rana sylvatica. The wood frog is the first member of its genus to breed. In spring shortly after the melting of the ice (usually the middle of March in the vicinity of New York City) the adults collect in woodland pools where their eggs are deposited in a firm oval jelly mass, in water that averages 10° . The wood frog is the most northerly distributed of our eastern frogs. In Canada it is represented by the closely related variety, *R. sylvatica cantabrigensis* (see Trapido and Clausen, '38). This, or a similar form, has been taken as far north as $67^\circ 30'$ on the Mackenzie River by Preble ('08).

In view of the early breeding habits and northern distribution one might expect the eggs of this form to tolerate extreme cold, and indeed this is so. It has been customary to keep the eggs at $2.5 \pm 1.0^\circ$ and subsequently use the embryos in transplantation experiments. Eggs placed in the cooling unit of the refrigerator for 12 hours developed normally after being returned to 20° even though a layer of ice had formed over the water. Although the eggs of this species can tolerate a lower temperature than those of any other frog investigated, they are the least resistant at higher temperatures. Eggs from four different females developed normally at $23.7 \pm 0.2^\circ$. Eggs from another gastrulated abnormally at $23.6 \pm 0.4^\circ$. Still another group died in stage 16 when kept at $24.5 \pm 0.2^\circ$. Finally at $27.2 \pm 0.2^\circ$ eggs from four different females died as blastulae.

TABLE I. Time in hours after first cleavage that eggs of *Rana sylvatica* were in various stages at different temperatures

Experiments	2	2	1	3	1
Temperature	10.0±0.6°	15.3±0.3°	18.5±0.2°	19.9±0.1°	23.7±0.2°
Stage 3	0	0	0	0	0
8	24	14-18.5		14.5	9
9	36	21-23	14-16		
10	48-52	24-29	17-18	16-20	
11	60-66	35	22-24	20-23	
12	72-84	37-48	26-30	23-26	17.5-21
13	96-114	47-50.5	34	37.7	
14	120-132	54-60	38	37.7	29
15	137	63-66		40.5	
16	144-162	67.5-73	49.5	40-45	
17	168-171	77-90.5	52.5- 54		35
18		84-101	57-70	50	41-43
19	228-304	108-113	73	66	47-50
20	282-327	123-132	87	72-87	52

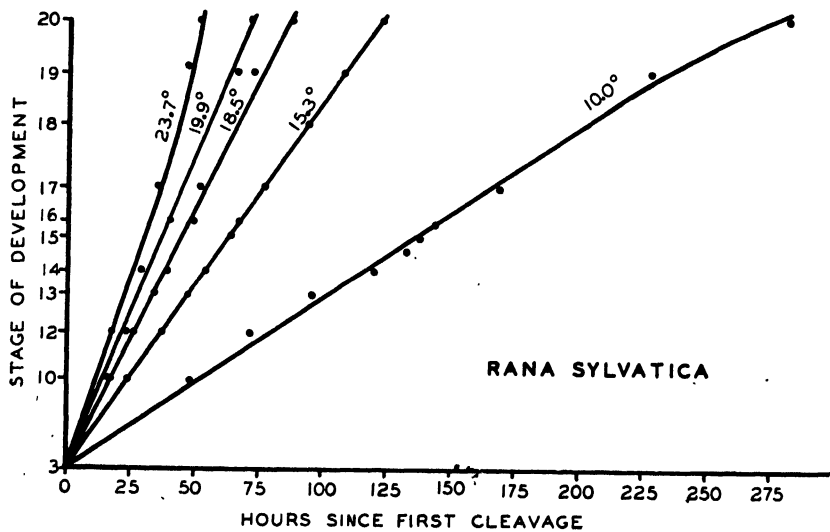


FIG. 1. The relation between temperature and rate of development in *Rana sylvatica*.

The eggs of this species develop (Fig. 1, Table I) more rapidly than do those of any other form studied. This rapid development is continued, and in from 50 to 60 days (maximally fed with egg yolk and spinach and kept at 20°) after first cleavage the front legs of the metamorphosing tadpoles appear. Adolph ('31) finds that at 19° the forelegs are acquired in 54 days. Under natural conditions from 61 to 115 days are required (Wright, '14).

Rana pipiens. This species generally breeds early in April near New York City (the best description of the breeding habits of the frogs used in

these experiments is to be found in Wright, '14). The temperature of water where the eggs are shed, averages 12° (Wright, '14). Preble ('08) found *R. pipiens* as far north as the sixtieth parallel in the region near Fort Smith. While existing records leave much to be desired, it appears that *R. pipiens* is found farther north than *R. palustris*, *R. clamitans*, or *R. catesbeiana*. It is not distributed as far north as *R. sylvatica*.

The eggs of *R. pipiens* used in these experiments averaged 1.7 mm. in diameter. They are somewhat smaller than those of either *R. sylvatica* or *R. palustris*. The oval jelly mass in which they are deposited lacks the firmness of that in the two latter species.

TABLE II. Time in hours after first cleavage that eggs of *Rana pipiens* were in various stages at different temperatures

Experiments	5	2	12	4
Temperature	15.3±0.1°	18.6±0.1°	19.8±0.2°	26.0±0.4°
Stage 3	0	0	0	0
4		1		
5		2		
8	13.5-21.7			7
9	24-29	19-20.5		
10	36-40	22-24	20-24	13.5
11	43.5	28-30	25	
12	48-59.5	32-41.5	29-37.5	16.5-19
13	67-68.2	45.7	38-44	21.5-24
14	73-84	48-54	43.5-48	27.5
15			50-54.5	
16	88-96.5	60-65	51-58	29
17	117-123.5	68-73	60-69	36-41
18	142	77-102	70-84	43-48
19	149-163	103-114	85-96	50-51
20	168	116	95-103	54-59

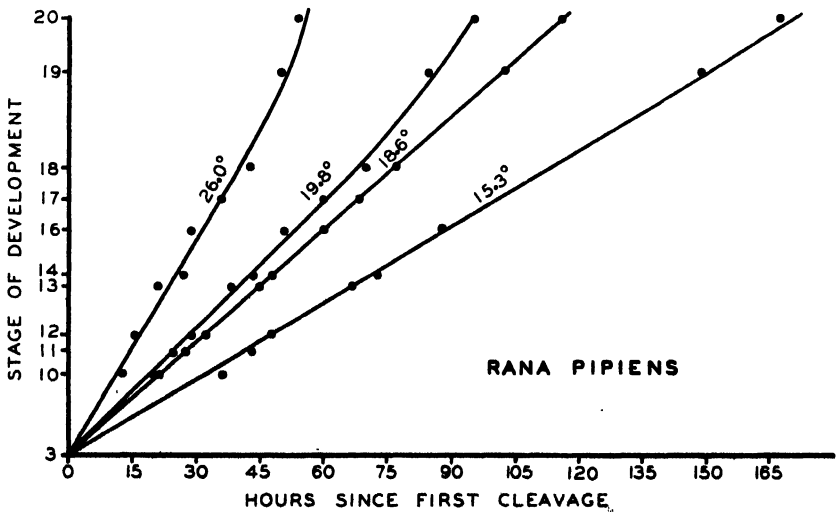


FIG. 2. The relation between temperature and rate of development in *Rana pipiens*.

The eggs are killed by temperatures as low as $2.5 \pm 1.0^\circ$. They cannot, therefore, tolerate as low a temperature as *R. sylvatica*. When kept at $5.0 \pm 1.9^\circ$ from stage 3 to 10, cleavage in the vegetal hemisphere was irregular, but in spite of this they developed into normal tadpoles when removed to 20° for the remaining time. Normal development occurred when the eggs were kept at $8.4 \pm 0.5^\circ$. Atlas ('35) found 5° to be subminimal.

The upper limiting temperature is approximately 28° . At $29.1 \pm 0.4^\circ$ over half of the eggs from one female developed abnormally. All those from another female formed abnormal tadpoles at $29.6 \pm 0.9^\circ$. In yet another case, however, perfectly normal tadpoles were produced at $30.0 \pm 0.3^\circ$. This latter case was probably exceptional as both Atlas ('35) and Hoadley and Brill ('37) find 29° supramaximal for development.

The effect of temperature on developmental rate in *R. pipiens* has been admirably treated by Atlas ('35). Since he did not use the same stages that are employed here, this form has been reexamined (Table II and Fig. 2). Development to stage 20 is 32 per cent slower than in *R. sylvatica* at 19.9° . The time required from egg to transformation at 19° is 117 days (Adolph, '31). Under natural conditions this occurs in from 71 to 111 days (Wright, '14).

Rana palustris. The next in order of breeding is the pickerel frog. Near New York City breeding occurs about the middle of April. Pond water at this time averages 14 to 16° (Wright, '14). This species has been taken at James Bay (51 – 54° N., Cope, '89). It was not recorded by Preble from west of Hudson Bay ('02), or in the Athabaska-Mackenzie region ('08), so evidently it does not range as far north as *R. pipiens* or *R. sylvatica*. The eggs average 1.85 mm. in diameter and are deposited in a firm oval jelly mass.

TABLE III. Time in hours after first cleavage that eggs of *Rana palustris* were in various stages at different temperatures

Experiments	2	2	2	2	1
Temperature	$15.5 \pm 0.2^\circ$	$18.6 \pm 0.1^\circ$	$19.9 \pm 0.2^\circ$	$25.7 \pm 0.5^\circ$	$30.4 \pm 0.4^\circ$
Stage 3	0	0	0–1	0	0
9	29	19–22		11.5	
10	35–43	24–30	20–24	13	11
11	51	32	29.5		
12	49–69	36–45	35	20–21	21
13	66–74	45–50	38–43	24	
14	80–92	52–60	46–55	30	24
15	96–98		55		
16	107	65–68	61–64	34.5–37.5	
17	103–138	73–78	66–74	42–43	34–42
18	138–170	89–114	80–83	49–52	48
19	167–180	119–124	95–98	56	
20	187–192	126	105–106	60–66	
21					60

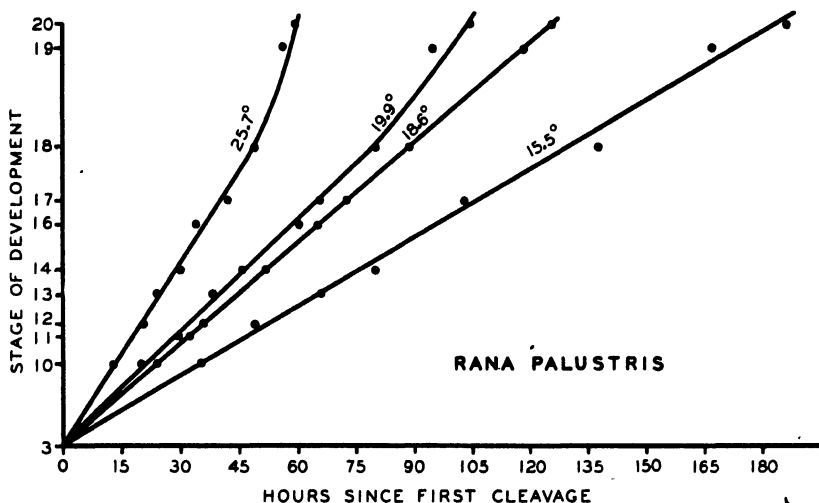


FIG. 3. The relation between temperature and rate of development in *Rana palustris*.

As in the case of *R. pipiens* eggs kept at $2.5 \pm 1.0^\circ$ are killed. Those in one experiment were killed at $5.8 \pm 0.7^\circ$. Normal development occurs at $8.6 \pm 0.5^\circ$. The maximum is near 30° . At $30.4 \pm 0.4^\circ$ most of the eggs from one female developed normally. At $31.9 \pm 0.1^\circ$ all died before gastrulation. The limits of temperature tolerance are similar to those of *R. pipiens*, but appear to be a degree or so higher. Neither *R. palustris* nor *R. pipiens* can withstand temperatures as low as *R. sylvatica*. The maximum of *R. palustris* is near 30° , compared with 28° for *R. pipiens*. However there is some overlapping as in one case the latter developed normally at $30.0 \pm 0.3^\circ$.

Development to stage 20 is 10 per cent slower than in *R. pipiens*, and 46 per cent slower than in *R. sylvatica*. The data for development are in Table III and figure 3. Under natural conditions the time from egg to metamorphosis is 90 to 100 days (Wright, '14).

Rana clamitans. The green frog, *R. clamitans*, breeds in late spring and early summer when the temperature of pond water averages 25° (Wright, '14). It does not extend as far into Canada as the earlier breeding species, but it has been taken as far north as Lake Nipigon, Ontario (50° N.) by Logier ('28), and in the Lake Abitibi region (49° N.) by Dymond ('28). The eggs used in these experiments averaged 1.4 mm. in diameter. They are normally deposited in a surface film, rather than in the partially or completely submerged compact mass characteristic of the early spring breeders.

Eggs kept at $4.7 \pm 0.3^\circ$, and at $10.0 \pm 0.3^\circ$ were killed before gastrulation. At $12.2 \pm 0.5^\circ$, and temperatures up to and including $33.4 \pm 0.2^\circ$, normal development takes place. At $36.1 \pm 0.3^\circ$ the eggs die as blastulae. The upper limiting temperature therefore is near 35° .

The rate of development (Table IV; Fig. 4) is slower than in any

TABLE IV. Time in hours after first cleavage that eggs of *Rana clamitans* were in various stages at different temperatures

Experiments	2	1	2	1
Temperature	15.0±0.3°	19.8±0.2°	25.3±1.0°	33.4±0.3°
Stage 3	0	0	0	0
7	6			
8	18-32			
9			6	
10	44-50	20-22		
11	50-55	25		
12	56-80	33	18-22	
13	93		23.5	
14	97	43-50	26.2	
15	109		28	
16	111-125	53-56	32	22
17	141-164	67-72		
18	164-200	73-93	42-45	31
19	215-222	97-111	50-56	
20	238-287	112	58-65	45

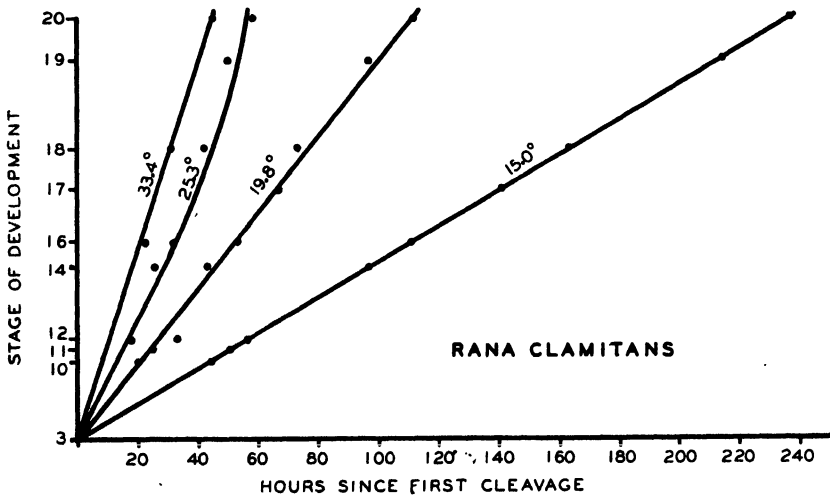


FIG. 4. The relation between temperature and rate of development in *Rana clamitans*.

species treated previously. At 19.9° development to stage 20 is 57 per cent slower than in *R. sylvatica*, 19 per cent slower than *R. pipiens*, and 7 per cent slower than *R. palustris*. Under natural conditions *R. clamitans* does not transform until one year after the beginning of development. This is in marked contrast to *R. sylvatica*, *R. pipiens*, and *R. palustris* all of which transform in several months.

Rana catesbeiana. The bullfrog, *R. catesbeiana*, is the last member of its genus to breed in this region. Correlated with this, its northern distribution is less extensive than is that of any of the forms previously described. It is absent from the Gaspé Peninsula (48° N.), Lake Nipigon (50° N.,

Logier, '28), and Lake Abitibi (49° N., Dymond, '28). Toner and Edwards ('38) found it common at Grippen Lake, Leeds County, Ontario (44° 30' N.). Cox ('98) found it in New Brunswick, and Coventry ('31) reported it from the Temgami District (47° N.).

The eggs are similar to those of *R. clamitans* in size and are likewise deposited in a surface film.

TABLE V. *Hours of development of the eggs of Rana catesbeiana, Bufo americanus, and Bufo fowleri in the various stages*

	<i>Rana catesbeiana</i>	<i>Bufo fowleri</i>	<i>Bufo americanus</i>
Experiments	1	1	1
Temperature	18.5°	19.9±0.2°	19.9±0.1°
Stage 3		0	
7			0
8	0-4	10.5-12.5	
10	15-16.5	17	13
11	16.5-21		
12	24	22	16.5-21
13	34.5		27
14	50		39
16	63.5		45
17	73	58	61
18	88-113	70	
19	118-149	94	74
20	159	107	85

No observations have been made on the temperature tolerance of the eggs of this form. The data on development (Table V) were gathered by Dr. Pollister and Dr. Barth. They have very kindly allowed me to use their observations to supplement the material already presented. They found the time from stage 8 to 20 to be 159 hours at 18.5°. At this temperature 170 hours would be a fair estimate of the time from stage 3 to 20. With this value we can compare the rate of development with that of the other forms (as read from the curve in figure 6). *R. catesbeiana* is then 95 per cent slower than *R. sylvatica*, 46 per cent slower than *R. pipiens*, 35 per cent slower than *R. palustris*, and 27 per cent slower than *R. clamitans*. *R. catesbeiana* has the longest larval period of any species in northeastern North America. The tadpole does not transform until the second summer after the beginning of development (Wright, '14).

COMPARISONS

In the previous section it was shown that those frogs characteristic of northern regions, and which breed early in the year when environmental temperatures are low, differ from species characteristic of more temperate conditions as follows:

1. In being able to tolerate lower temperatures in the egg and larval stage, and being more susceptible to higher temperatures.
2. In compensating for the retarding effect of the low temperature of their environment by a rapid rate of development.

The limits of temperature tolerance are shown in figure 5. It will be seen that the eggs of all four species are not able to develop over the same wide range of temperatures, but each species is adapted to a narrower range which covers the conditions existing in its particular environment at the time of breeding. It is also of interest that the number of degrees over which normal development occurs (difference between the upper and lower limiting temperatures) is practically identical, being 22–24°.

A comparison of the rates of development of these same four species is made in figure 6. *R. sylvatica* which is best adapted to cold with respect to temperature tolerance in early stages, has the most rapid rate of development. Species breeding later when the surrounding pond water is warmer develop progressively slower. It will be seen from the curves that the difference in rate is most apparent at low temperatures. This will be discussed later.

A summary of the various correlations so far presented is given in Table VI. The values for the upper and lower limiting temperatures are somewhat approximate. Thus in the case of *R. clamitans*, the lower limit for development is placed at 11°, as 10.0° is too low for normal development, but 12.2° is quite suitable. Likewise these same eggs develop at 33.4° but are killed at 36.1°. The upper limiting temperature is then placed at 35°.

RESULTS ON OTHER GENERA

The fact that the range of temperature tolerance of frog eggs is similar to the environmental temperatures to which these eggs are subjected in nature

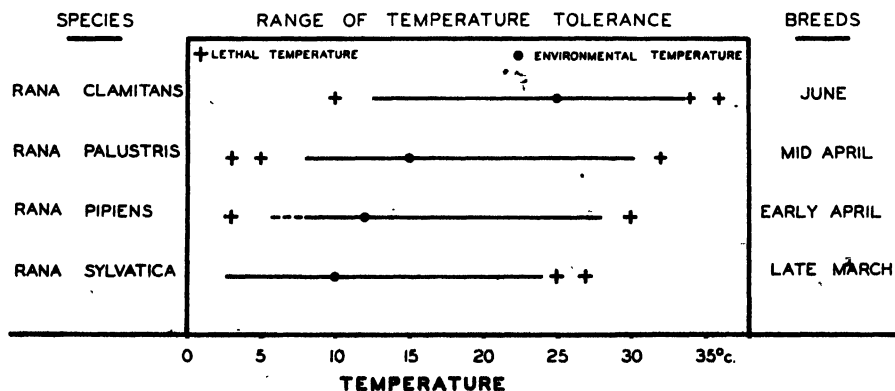


FIG. 5. The relation between temperature tolerance and breeding habits in frogs. The heavy black lines indicate the temperatures at which normal development takes place. Lethal temperatures are indicated by crosses. The average water temperature at the time of egg-laying is indicated by the dot on the temperature tolerance line.

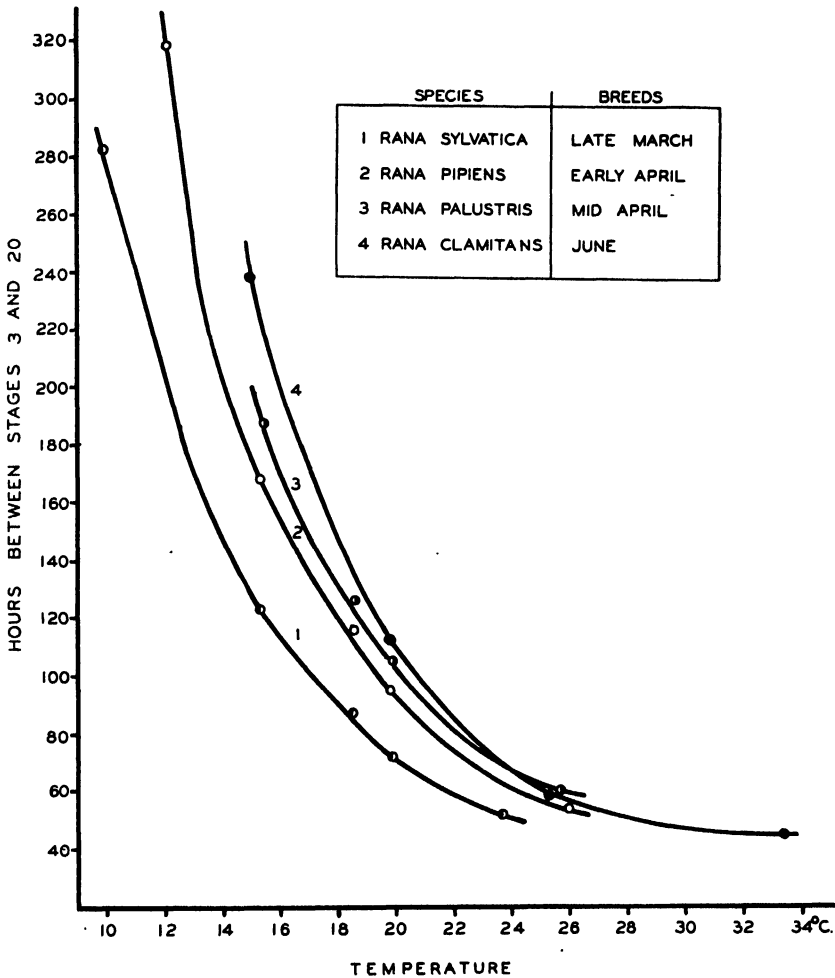


FIG. 6. A comparison of rate of development between four species of frogs. The curves represent the time to reach stage 20 at several temperatures.

is not surprising. Quite regularly also, animals that can withstand low temperatures, but cannot endure high temperatures, are more northern in their distribution than those with higher maximal and minimal embryonic temperatures. The significance of the rapid rate of development of northern animals however is not so apparent. Therefore, preliminary experiments have been carried out on two additional genera of Amphibia to learn if the rapid rate of cold-adapted species is of common occurrence in this group.

Bufo. *Bufo americanus* breeds in April in the New York City region. It ranges far to the north, having been reported from the Labrador Peninsula (Speck, '25), and throughout much of Canada. The Canadian form has been separated as *B. americanus copei* Yarrow and Henshaw by some authors.

TABLE VI. *Comparison of breeding and development of various species of Rana*

	<i>R. sylvatica</i>	<i>R. pipiens</i>	<i>R. palustris</i>	<i>R. clamitans</i>	<i>R. catesbeiana</i>
Order of breeding	1	2	3	4	5
Water temperature at time of breeding	10°	12°	15°	25°	
Most northern record	67°30'N.	60°N.	51-55°N.	50°N.	47°N.
Lower limiting embryonic temperature	2.5°	6°	7°	11°	
Upper limiting embryonic temperature	24°	28°	30°	35°	
Time between stages 3 and 20 at 18.5° C.	87	116	126	138	170

B. fowleri breeds in May in the New York City region, and extends only to southern Canada. Wright and Wright ('33) have described this as an Upper Austral species, which in a given locality breeds later than the Transitional and Canadian Zone form, *B. americanus*.

The rate of development of these forms is given in Table V. It will be seen that the data are not extensive but are sufficient to show a difference in rate. The experiment on *B. americanus* was begun when the eggs had just entered stage 7. The time between stages 3 and 7 at this temperature could not have been more than 5 hours. This would mean that *B. fowleri* requires about 107 hours from first cleavage to gill circulation (stage 20), and *B. americanus* 90 hours or less. Here again we find that a species which breeds earlier than another of the same genus, and which is distributed farther to the north, has a more rapid rate of embryonic growth.

Ambystoma. The limits of distribution of *Ambystoma* are even more imperfectly known than in the case of the frogs and toads. *A. jeffersonianum* seems to be the characteristically northern species. Cope ('89) records it from James Bay. *A. maculatum* has not been taken this far north but it does occur throughout south-eastern Canada. *A. tigrinum* reaches Canada only in the central region. *A. opacum* does not extend north of New England. Both *A. tigrinum* and *A. jeffersonianum* lay before *A. maculatum*. As they rarely occur under similar conditions it is not possible to say which of these two is the earlier breeder. *A. maculatum* breeds during the last half of March in the New York City region. *A. opacum* breeds in late September and early October in the same region. The temperature of ponds where *A. maculatum* lays has varied from 6° to 12°. Presumably it is somewhat lower when *A. tigrinum* and *A. jeffersonianum* spawn as they do so earlier in the season. The mud nests of *A. opacum* have varied from 16° to 18° when the eggs are first laid.

The observations on rate of development are given in Table VII. The

eggs of *A. tigrinum* are from two sources, those collected on Long Island, and others from the neotenic axolotl kept in laboratory tanks. Observations on those collected under natural conditions were not begun until the end of gastrulation. As the rate from this time on is indistinguishable from that of the axolotl, it is thought legitimate to use the more extensive data of the latter as representative of the species. Observations on *A. jeffersonianum* were begun when the eggs were just beginning to gastrulate. They pass through subsequent stages more rapidly than do any other species examined. This is of interest when we recall it to be the typically northern member of its genus. *A. tigrinum* develops somewhat more slowly. *A. maculatum* develops still more slowly, and *A. opacum* which lays its eggs under the warmest conditions has the slowest rate of development of any.

In figure 7 the rates of development are compared. The data for the axolotl are used as a base line. Twenty-four hours have been added to the times for *A. jeffersonianum* so that they may be compared with the other species. This amount represents the time required by *A. tigrinum* to reach stage 10 and is a conservative estimate, as in subsequent stages *A. jeffersonianum* develops more rapidly. The scatter of the points is due in part to the difficulty of referring embryos of all species to Harrison's stages made especially for *A. maculatum*.

TABLE VII. *Hours of development of the eggs of various members of the genus Ambystoma as noted in Harrison's stages*

	<i>A. macu- latum</i>	<i>A. jeffer- sonianum</i>	<i>A. opacum</i>	<i>A. tigrinum (axolotl)</i>	<i>A. tigrinum</i>
Experiments	3	1	1	3	1
Temperature	19.9±0.1°	19.9±0.1°	19.9±0.1°	19.9±0.1°	19.9±0.1°
Stage 2	0		0	0	
7	14			10	
8	16		20	14-22	
9	31-36				
10	42	0	40	24-25	
11	49.5		50	34	
12	53-55.5	4-9	60		
13	63-64	11	80	46-55	0-10
14	72-74	21			13
15	77.5	24	85	58	
16		26			
17	82				
19	88	28			
21		31	110	65-68	
23				69-72	23
24			130	76	
26	122	47	140	83	37
29				87	48
30				94	
31	146				
Heart beat	168	80		120-127	82
Gill circulation		99		146-153	106

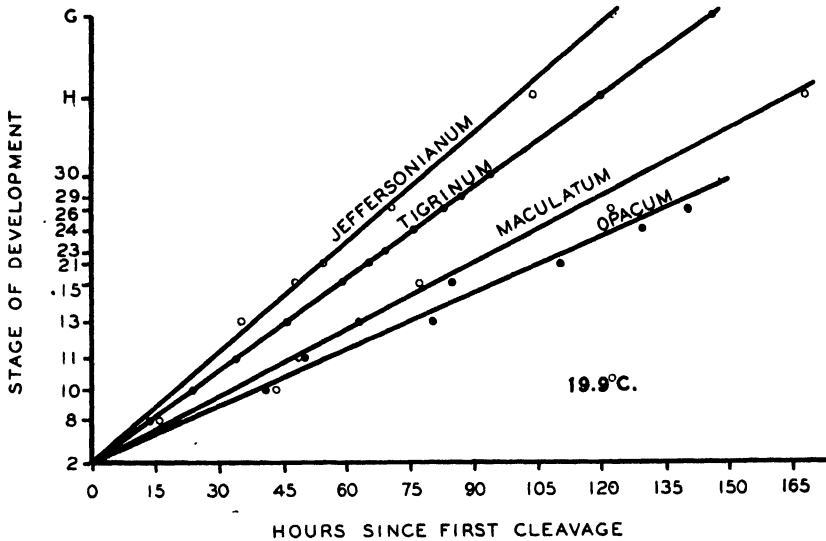


FIG. 7. A comparison of rate of development between four members of the genus *Ambystoma* at a common temperature.

The correlation between breeding conditions and rate of development shown to exist in the genus *Rana* likewise holds in these salamanders. Those species which lay their eggs early in the season when it is cold, and are more northern in their distribution, develop more rapidly than those which spawn later, and which may be considered southern species.

DISCUSSION

In previous investigations it has been noticed that variations in temperature tolerance of the eggs of different amphibians are correlated with the environmental temperature at the time of breeding, though these observations are fragmentary. Lillie and Knowlton ('97) found *Ambystoma tigrinum* more resistant to cold than *Rana pipiens*, as was pointed out previously. Hertwig ('98) found 24° to be the upper limiting temperature for the early breeding *R. temporaria*, whereas in the case of *R. esculenta* which breeds in May and June, it is 32–33°. Morgan ('02) noticed that the eggs of *R. sylvatica* were not affected by a sojourn in his ice cabinet, while those of the later breeding *R. palustris* were injured. Miss King wrote ('03), "it may be possible to show, after more species have been studied, that the maximum temperature which eggs of amphibians can endure without injury and also the temperature most favorable for their development depend, to a certain extent at least, on the time of the year at which the eggs are deposited." As can be seen in figure 5 the convictions of these earlier investigators have been substantiated.

This relationship of course is not surprising and it has been noticed in

many animal groups (Runnström, '28). It would be difficult to conceive of a species flourishing in a region where the existing temperature is lethal to any stage in its life history, unless its status is maintained by immigration from more favorable localities.

It seems, therefore, that each species of frog is best adapted to a particular geographic range, and to a special breeding season, in which conditions are suitable for development of the eggs. It is not a case of all the frogs studied being able to tolerate temperatures within a wide limit during early development, but each species is able to develop normally over a smaller range of temperatures covering conditions during the time of breeding. Hörstadius ('25) has even shown that eggs of the same species may have different temperature limits when laid at different times during the year. Thus the eggs of the sea urchin *Paracentrotus lividus* develop normally from 8° to 23° in winter when ocean temperatures are 13°, but during the summer months when the temperature has risen to 26°, the lower temperature limit is 16°, and the upper limit is 29°.

It is of interest to note that marine animals are not able to withstand as wide a range (difference between the upper and lower limiting temperatures) of temperatures as the four species of *Rana*. *Paracentrotus lividus* is able to develop normally over a range of 16° in the winter and 14° in the summer (Hörstadius, '25). Runnström ('27) examined the eggs of twelve species belonging to several phyla and found the greatest range to be 16°, and the smallest range over which normal development occurred to be 12°. On the other hand, all of the frogs are able to develop over a range of 22–24°. This greater range for frogs is doubtless correlated with the eurythermal condition of a fresh water environment, in contrast to the more constant temperature of the ocean.

The relation between temperature tolerance and rate of development has been discussed by Zawadowsky and Sidorov ('28). A survey of the literature showed them that some species could be arranged according to the velocity of cleavage in the egg. Those with the most rapid segmentation had a lower temperature tolerance and a lower Q_{10} , a relation similar to that shown to exist in frogs. To test this concept they studied the temperature tolerance and rate of development in *Ascaris megalocephala*, *A. suilla*, and *Toxascaris limbata*. They did not find support for their original hypothesis. However, their material was not especially satisfactory, and the difference in temperature tolerance among these parasitic species is very slight.

In the investigations on Amphibia the relation between temperature tolerance (and breeding time) and rate of development is too regular to be explained on a chance variation basis. Species adapted to northern conditions consistently have a more rapid rate of development than southern forms. Low temperature, however, is not the only environmental factor correlated with rapid growth. Amphibians that lay their eggs in temporary pools and

puddles must of necessity have short larval periods if they are to transform before these bodies of water disappear (Ju-Chi Li, '34; Trowbridge and Trowbridge, '37). Also amphibians found in semi-arid regions have a more rapid rate of development, according to Storer ('25). In eastern North America, however, there is an abundance of water in the spring and the differences in rate of development seem best correlated with temperature. As in the case of forms breeding in temporary bodies of water, and in semi-arid regions, the temperature effect is perhaps an adaptation to the length of time breeding sites are available, especially in the northern portion of the species' range. A form like *Rana sylvatica*, for example, can breed in March in the latitude of New York as the ponds are then free of ice, but at increased latitudes the time of the spring thaw becomes later and the winter freeze comes earlier, with the result that ponds are open for a shorter period during which embryonic growth can take place. It is thus conceivable that forms having a long larval period are better adapted to more temperate conditions. This has been shown by Zschokke ('00), who found a correlation between the length of larval life and the altitudinal limit of amphibians in the Alps. Here an increase in altitude results in a reduction of the growing season as does an increase in latitude. *Rana temporaria* with a larval period of 85–95 days reaches an altitude of 2500–2600 meters. *Hyla viridis* with a larval period of 80–98 days reaches 2200 m. *Bufo vulgaris* ranges to 2000–2100 meters. Its larval period consumes 110–120 days. *Alytes obstetricans* and *Bombina bombina* with larval periods of 120–130 and 124–134 days respectively, reach 1500–1650 and 1200–1500 meters. It would seem therefore that amphibians with long larval periods are not characteristic of regions where the ponds are free of ice for but a short time.

There are a number of cases in the literature, some of which will be cited, that indicate northern, or cold adapted species, have a more rapid rate of development at the temperatures of their environment than southern forms at these same low temperatures. Hertwig ('98) found *Rana temporaria* to develop more rapidly than *R. esculenta*. The former has a lower range of temperature tolerance and extends farther north. Races of *Lymnættria dispar* from the northern part of Europe and northern Japan develop more rapidly than races from southern Europe and Turkestan (Goldschmidt, '33). Ide ('35) has shown very clearly that those species of *Ephemeroptera* characteristic of cold waters grow more rapidly under natural conditions than those found in a warmer environment. Loeb ('16) found segmentation to be more rapid in *Strongylocentrotus* than in *Arbacia* at low temperatures. The former is a characteristic species north of Cape Cod, whereas *Arbacia* is the common sea-urchin south of the Cape. Geisthardt ('37) finds the European *Cimex lectularius* to have a shorter larval period than the African *Cimex rotundatus*. The optimum temperature for development of *Cimex lectularius* is 27°, and for *C. rotundatus*, 29°. Fox* ('39), who is especially interested in this prob-

lem, found the rate of segmentation in the northern *Psammochinus miliaris* to be greater than in the Mediterranean *Psammochinus microtuberculatus*.

It is suggested, other factors being constant, that animals characteristic of northern, or cold regions, have a greater growth rate at the temperatures of their environment than closely related southern forms at these same low temperatures. Orton ('23) has expressed a similar view, thus he states, "it does not necessarily follow that because the rate of metabolism in tropical or temperate animals falls off rapidly with decreasing temperatures approaching 0° C., that metabolism in polar animals is necessarily of the slow rate of temperate animals at polar sea-temperature. No reason has yet been shown that adaptation of metabolism cannot occur; on the contrary there is every reason to expect such adaptation." Whether this correlation is as universal as the other rules expressing regularities in geographical variations (Dobzhansky, '37) remains to be seen.

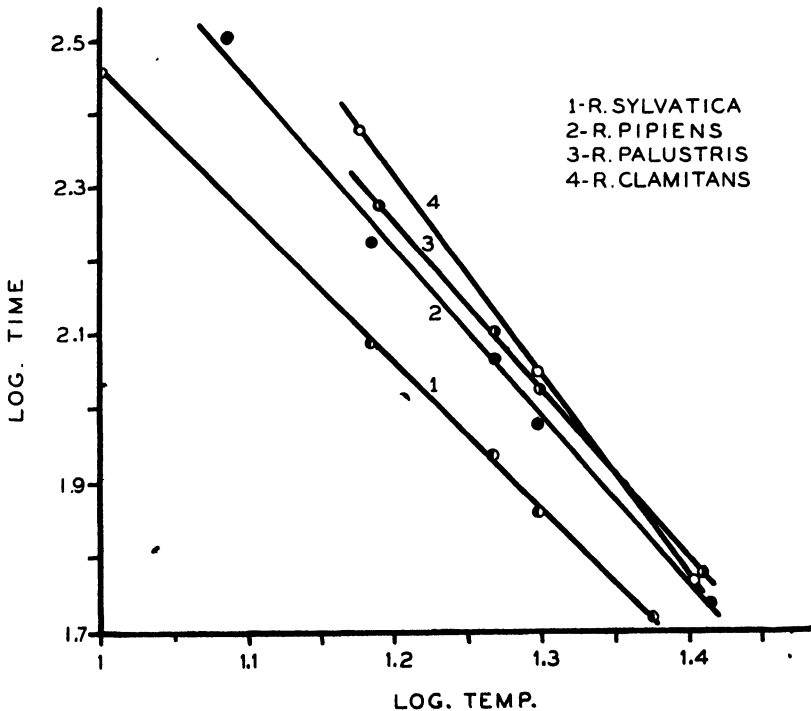


FIG. 8. A log. plot of the data in figure 6.

We have pointed out previously that the differences in rate of development are greater at low temperatures. This becomes more apparent when the data on time to reach stage 20 (Fig. 6) are plotted as logarithms (Fig. 8). It is then seen that not only is the entire curve shifted to the right with an increase in temperature tolerance, but the slope is greater. This increase in

the slope of the curve may even result in a slightly greater rate of development. Thus at temperatures above 25° *Rana clamitans* reaches stage 20 in less time than *R. palustris*, whereas at lower temperatures the latter develops much more rapidly. Loeb ('16) noticed this in a comparison of segmentation rates in *Arbacia* and *Strongylocentrotus*. At low temperatures the northern *Strongylocentrotus* develops more rapidly, but at temperatures above 15° this order is reversed. Bělehrádek ('35) has discussed the relation between temperature tolerance of eggs and his temperature coefficient b (value for the slope of the line representing the time to reach a given morphological stage at a number of temperatures in a log-log plot). The data given in this paper confirm his hypothesis that "the temperature coefficient of analogous biological processes increase with the adaptation of the protoplasm to higher temperature." The value of b for *Rana sylvatica* with an upper limiting temperature of 24° is 2.0. For both *R. pipiens* with an upper limiting temperature of 28° (but see notes under "Experimental"), and *R. palustris* with an upper limit of 30°, b is 2.3. The value of b in the case of *R. clamitans* which can tolerate temperatures as high as 35°, is 2.6.

A point of interest in the figures for development of each species (Figs. 1-4) is the apparent divergence of some of the curves at advanced stages. This increase in the value of the temperature coefficient with the stage of development reached, has been noticed by other investigators and is discussed by Bělehrádek ('35). The significance is not known.

SUMMARY

1. A correlation was found to exist between breeding habits of Amphibia, their geographical distribution, and the temperature tolerance and rates of development of the eggs (Table VI).
2. Frogs breeding when environmental temperatures are low have lower minimal and lower maximal temperatures than species breeding when pond water is warmer.
3. The range (difference between upper and lower limiting temperatures) over which normal development is possible is 22-24° in the four species of frogs studied.
4. Frogs, toads, and salamanders breeding when temperatures are low develop more rapidly than forms breeding under warmer conditions.
5. The early breeding species are in general more northern in their distribution than forms breeding later.
6. The temperature coefficient of development is lower in northern species than in southern species of frogs.

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ENVIRONMENT AND PHYSIOLOGICAL ACTIVITIES OF WINTER WHEAT AND PRAIRIE DURING EXTREME DROUGHT *

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INTRODUCTION

This study is the third of a series on the comparison of environments and development of crop plants and native vegetation. The first (Flory, '36) dealt with maize and upland prairie; the second (Fredricksen, '38) is a comparison of alfalfa and native grassland. The present paper deals with winter wheat and native upland prairie. This research also completes the twenty-first year of a continuous study of the major environmental factors of air and soil in the most extensive and most productive plant formation in North America (Weaver and Himmel, '31).

With the settlement of the prairie, chief attention was given to breaking the sod and the production of crops, with little thought of changes produced in the environment, although it was commonly believed that such procedure increased rainfall. Later, attention was focused upon the effects of various crops and crop rotations, primarily upon production but in part upon soil depletion. Little thought was given to natural environment and the stabilizing effect of grassland until problems besetting the plant producer became increasingly complex and were further aggravated by periods of great drought. We are now much concerned with changes in soil profile; with soil losses by accelerated erosion; with soil movement by great dust storms; in fact, by all the changes that have occurred in the brief span of years since the removal of the original cover that has characterized the grassland formation for several million years. Only by projecting present conditions against the background of prairie that still persists with little change, can we fully understand the direction and degree of departure from conditions long established by nature (Smith, '32; Weaver and Flory, '34).

This work was done during a year of the most extreme drought that has ever been recorded in eastern Nebraska. It afforded an unparalleled opportunity to measure extremes of differences in a natural and a cultivated habitat and to study the behavior of both native and crop plants under the most adverse conditions.

This study is a comprehensive comparison of the environment and certain physiological responses of native grassland vegetation and winter wheat.

* Contribution No. 118 from the Department of Botany, University of Nebraska.

Environmental factors were quantitatively determined in the two habitats from the planting of the wheat, September 25, 1933, to harvest in 1934, and in the stubble field and prairie until the following September. They included atmospheric factors of precipitation, humidity, temperature, wind, and evaporation. Soil structure, hygroscopic coefficients, and pH of the soils at different depths were determined. Continuous records of soil temperatures were obtained, runoff was measured, and water content was determined weekly to a depth of four feet. The physiological responses measured were rate of water loss by phytometers, rate of growth as determined by increase in height and leaf surface, and production of dry matter.

DESCRIPTION OF THE AREA

The prairie and field lie three miles north and one mile west of the University of Nebraska in Lincoln. They consist of a gently rolling tract of land one-half mile long, from north to south, and nearly one-half mile wide. The plowed field, planted to wheat, included an area 30 rods wide and one-half mile long. The unbroken prairie occupies the remainder of the tract, except that the west one-half has been grazed, but only moderately, for several years. The pasture formed a buffer to the prairie which occupied a width of 20 rods throughout the full length of one-half mile. A small ravine crosses both field and prairie from east to west about one-third of the distance from the south end. The stations were established on the gentle south slope of the land just north of the ravine. Thus the area of both field and prairie was extensive enough to eliminate largely the influence of neighboring habitats. The southerly winds blew over a considerable area of prairie or wheat field respectively, before encountering the instruments and plants at the respective grassland or field station. Thus normal temperatures, humidity, and evaporation for each microclimate were attained (fig. 1).

SOILS

The soil is Carrington silt loam, a type common and extensive in eastern Nebraska. It has the profile of a mature soil. The *A* horizon is dark in color, fairly rich in humus, and extends to a depth of about 18 inches. The upper portion is disturbed in the field by repeated cultivation. At 12 inches depth the soil becomes lighter in color, and the silty clay loam of the surface 12 inches grades into clay. The *B* horizon extends about 18 inches deeper. It consists of a yellowish clay which is plastic when wet but very hard when dry. The prismatic structure is well developed and during drought there is great shrinkage among the vertical columns. The *C* horizon occurs at about 32 inches depth. While there is an entire absence of coarse grains of sand to this depth, the sand component consisting wholly of very fine sand, in the *C* horizon the clay gradually becomes intermixed with an increasing proportion of sand. At 8 to 9 feet in depth the subsoil becomes sandy.



FIG. 1. General view of stations late in October, '33.

The hygroscopic coefficients of the soil at the several depths to 6 feet are given in table I, where the pH is also recorded. The difference in the hygroscopic coefficients of the surface soil may be due to the smaller humus content in the field. The soils are slightly acid in the first 3 feet due to the leaching of the carbonates throughout the centuries. The mildly acidic condition prevailed in the field to the depth of sampling at 6 feet. They are fairly representative of upland soils of eastern Nebraska.

TABLE I. *Hygroscopic coefficients and pH of soils of prairie and field*

Depth	Prairie per cent	Field per cent	Prairie pH	Field pH
0''- 4''	10.8	8.8	6.0	5.6
4''-12''	10.7	11.8	6.0	5.8
1'- 2'	13.1	13.0	6.2	6.0
2'- 3'	14.7	12.8	6.9	6.0
3'- 4'	13.4	11.5	7.8	6.5
4'- 5'	12.7	12.1	7.8	6.5
5'- 6'	10.9	12.1	7.5	6.8

VEGETATION

The vegetation of the prairie is the typical, upland, mid-grass type, such as has been fully described by Weaver and Fitzpatrick ('34). It has a basal cover of about 13 per cent. Little bluestem, *Andropogon scoparius*, is the chief dominant, constituting 60 per cent of the vegetation.

The grasses normally reach a general level of 12 to 18 inches in July, when the vegetative growth is nearly complete. A lower layer consists chiefly of forbs but also includes minor grasses and sedges. The upper layer, culminating at about 2.5 feet in height, consists largely of autumnal blooming forbs. The foliage cover is 75 to 100 per cent during a normal season. Light intensities are often reduced to 3 to 8 per cent at the soil surface. The new vegetational cover of mostly long-lived perennials forms each year a protective blanket effectively screening the soil from direct insolation (fig. 2).

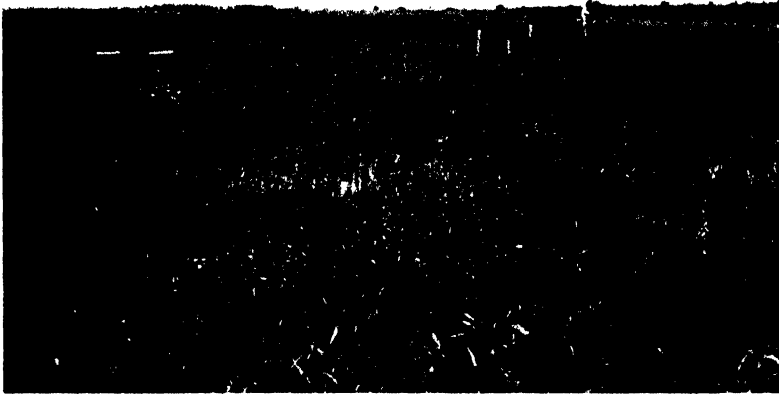


FIG. 2. General view of the prairie in June, with some phytometers withdrawn for weighing.

The field for wheat had been under cultivation for 30 years. The two preceding crops were wheat. Plowing in August followed by disking and harrowing had not only resulted in an excellent seedbed but also one free from weeds. Turkey red winter wheat was drilled in rows 7 inches apart at the rate of 75 pounds per acre on September 25, 1933. This is the optimum time for seeding winter wheat in Nebraska (Kiesselbach, '25). Timely showers promoted prompt germination and a good stand.

WATER RELATIONS

Water is a controlling factor in the development of vegetation. Its availability is usually determined not only by precipitation, but also by plant cover and structure of soil. Intensity, duration, distribution, and nature of the precipitation are all significant. Increase or decrease of water content of the soil may be the direct outcome of the activity of the plant cover. Cover may promote percolation and prevent runoff, but it also dries the soil by absorption

and transpiration. Moreover, by intercepting rainfall it has a marked effect upon reducing efficient precipitation (Clark, '39). Water capacity of the soil is increased by the accumulation of humus. Growth and death of roots and rhizomes promote good structure in prairie soil. Cultivation modifies the structure of field soil, and thus alters the movement of water through it.

Precipitation

The mean annual precipitation over a period of 56 years is 27.6 inches. Approximately 79 per cent occurs from April 1 to September 30, and 29 per cent between May 1 and June 30. Such seasonal distribution of moisture is especially favorable to the growth of grasses, but because of the high temperature, losses by evaporation from the soil are greatly increased. After May first, much of the precipitation occurs as torrential thundershowers which may cause much runoff and erosion.

Rainfall was measured by means of a standard rain gauge installed between the field and prairie stations. The monthly precipitation was far below normal except when a total of 1.67 inches of rain fell early in December (table II). The winter was dry.

TABLE II. *Mean monthly precipitation and precipitation from October 1, 1933 to September 1, 1934*

Time	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Total
56 yrs.	1.88	1.07	.80	.64	.93	1.25	2.41	3.94	4.18	3.83	3.54	24.47
1933-'34	.09	.60	1.67	.25	.78	.80	.35	.49	2.47	.40	2.59	10.49

Late in February rain and snow amounting to .78 inch supplied slightly more water than could be absorbed by the partly frozen soil. Seven light showers fell in March. The heaviest rain in April or May was .24 inch. Five rains in June varied from .12 to .64 inch, the dry soil losing by runoff part of the water supplied by the heavier showers. Water afforded by seven showers of .09 to .82 inch during July and August was practically all absorbed in the prairie. The drought was temporarily broken by an .84-inch rain early in September.

Summarizing, during spring and summer there were three periods each of two or more weeks duration in which no moisture fell and only six times did rainfall exceed one-half inch. Total precipitation for the 11 months was 10.49 inches. Only 33 per cent of the usual precipitation fell during April, May and June. Such deficiency was critical for plant development.

Runoff

The plot method of measuring runoff was used in comparing the water lost from prairie and wheat field. Two parallel plots were selected in the

prairie and two in the field. They were on a five-degree slope, and not more than 50 feet apart. The crop of winter wheat was removed from one plot in the field by spading the soil 4 inches deep. The area is designated as fallow land. Weeds were not allowed to grow in this plot nor was it given further cultivation.

Each plot, which was 3 feet wide and 33.3 feet long and parallel with the slope, was enclosed by planed boards 6 inches in width. Full descriptions of the plots and interceptometers are given by Weaver and Noll ('35) who first used them, and by Fredricksen ('38) who later employed them in determining runoff from alfalfa.

Runoff was determined only when the soil was unfrozen, and rainfall is given in table III only when runoff occurred.

TABLE III. *Runoff from prairie, wheat field, and fallow land*

Date	Rainfall, inches	Percentage of runoff		
		Prairie	Wheat field	Fallow land
Dec. 2, '33	1.30	2.0	0.8	—
" 3, "	1.47	2.5	5.2	—
Feb. 24, '34	.28	1.3	4.0	—
June 8, "	.58	1.0	0.1	0.3
" 14, "	.87 ¹	0.2	7.0	1.1
" 22, "	.54	0.0	0.0	0.4
Aug. 7, "	.80	1.0	3.4	12.8
" 31, "	.74	0.1	7.9	18.4
Sept. 1, "	.65	1.8	48.2	55.3
" 3, "	1.01	0.4	15.5	30.5
Total	8.24	Ave. 1.2	8.7	11.2

¹ Wheat harvested June 9.

On December 2, when the crop of winter wheat stabilized the dry, loose field soil, the runoff from a 1.3-inch rain was less than that in the mowed prairie. A rainfall of 1.47 inches, on December 3, after the surface soil had been thoroughly wet, resulted in more than twice as much runoff in the field as in grassland. When the soil was again very dry (June 8, '34), the small loss in the prairie exceeded that in the field during a .58-inch rain. But on June 14 a rain of .87 inch resulted in greater water loss from both the field and fallow land. This was the dry summer of '34 when the wheat grew so poorly that the mature crop was only 18 inches tall. Growth in the prairie, however, was also far below normal.

The relatively heavy rains of August 31 and September 1 resulted in high runoff except in prairie. Water lost from the fallow land considerably exceeded runoff from the wheat stubble. Practically all of the water from the inch of rain on September 3 was absorbed in the prairie, 15.5 per cent ran off the stubble field, and twice this amount from the fallow land. Losses of soil by erosion from these rains in the two field plots aggregated 296 pounds and 1,085 pounds per acre, respectively.

Water Content

Available water is considered as the percentage of water content in excess of the hygroscopic coefficient (Alway, '13). It was generally low not only because of the deficient current precipitation but also because of low water content, especially in the deeper soil, at the beginning of the experiment.

In the surface four inches, during the autumn, available water content in the field varied from 8.2 to 14.4 per cent; in the prairie from 8.2 to 17.7. During the winter period, December 3 to April 3, the available moisture in the field ranged from 11.4 to 30 per cent; in prairie from 21.5 to 30.1. Cultivating the soil exposed a greater surface to evaporation. The growing crop of wheat, moreover, continued to remove water by absorption and transpiration during the mild winter while the prairie plants were nearly all dormant and furnished a protecting cover of dead vegetation. Therefore, the water content was consistently higher in the prairie soil (fig. 3).

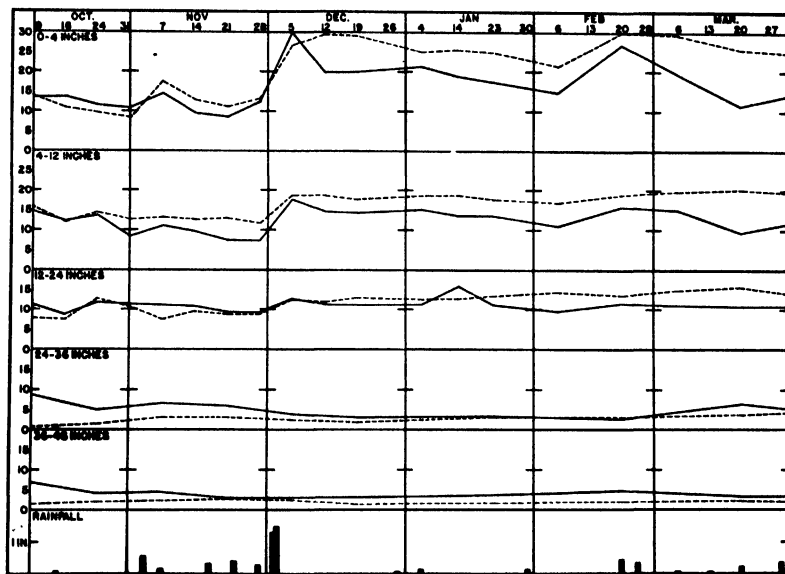


FIG. 3. Water content of soil in wheat field (solid line) and prairie (broken line) at the several depths to 4 feet during fall and winter of '33-'34. The precipitation is shown in inches.

Available water in the surface layer decreased rapidly during April (fig. 4). None was available in the field after April 24, except during two weeks in June and two different weekly periods in August. Water content in prairie decreased to the hygroscopic coefficient three weeks later than in the field. It was available for only one week in June but during three weeks in August. The largest amount available during the summer was only 7 per cent. The greatest deficiency in both field and prairie occurred in July, when intensive

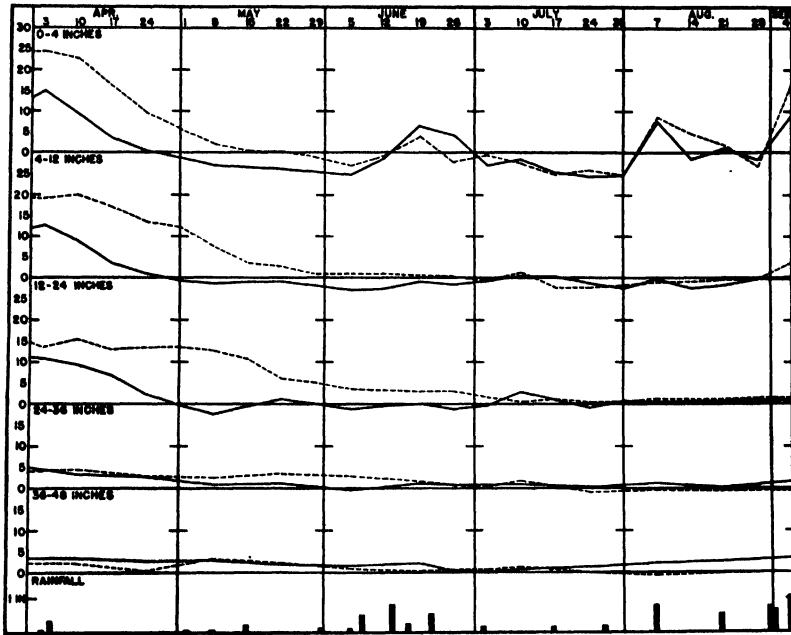


FIG. 4. Water content of soil in wheat field (solid line) and prairie (broken line) at the several depths to 4 feet during spring and summer of '34. Rainfall is shown in inches.

surface evaporation reduced the moisture 4 to 6 per cent below the hygroscopic coefficient.

At 4 to 12 inches depth, the highest moisture content in the field during autumn was 14.3 per cent on October 9, and the lowest 7.7 per cent on November 28. The prairie soil remained almost constantly at about 13 per cent (fig. 3). Rains of early December increased available water for the winter period. Field soil had a maximum of 17.7 per cent, but this decreased to 9 per cent by April 10, and more rapidly thereafter. Soil moisture in prairie was maintained between 16.7 and 20.4 per cent until April 10, after which it also rapidly decreased. Water became unavailable in the field on April 24 and remained thus until September 4. In the prairie, available moisture decreased gradually until there was only 1 per cent on May 29, an amount that prevailed until about June 26.

Available water content in the second foot varied between 7.7 and 15.8 per cent until April 10. Thereafter the field soil was in general slightly more moist than that of the prairie until late fall, after which, probably due to more surface soil evaporation and transpiration in the field, the prairie had continuously 3 to 5 per cent more available water. After the renewal of growth, water content decreased gradually in the prairie until on July 10 all available moisture was exhausted. The wheat exhausted the available water supply by May 1, ten weeks earlier than the prairie. Since little rain fell, slight

irregularities in the course of the graph are undoubtedly due to water penetration to this level through deep cracks in the soil (fig. 5). After May 1, the soil was continuously dry.



FIG. 5. Detail of soil in wheat field on May 25, '34, showing the network of deep cracks and the poor growth of the wheat resulting from the drought.

In the third foot, during fall and winter, slightly more water was usually available in the field than in the prairie. A similar condition maintained in the four-foot level. At no time did water content exceed 8 per cent and it was usually less than 5 per cent in both habitats. Upon resumption of growth, water in the field was exhausted about two weeks earlier than in the prairie. This phenomenon was not so well defined at four feet. After harvest, prairie plants continued absorption at these levels which accounts for lower water content here than under the dried stubble.

Summarizing, available water content was low in the third and fourth foot in both field and prairie during fall and winter. It became nonavailable during the following summer. In the first two feet there was 7 to 30 per cent moisture available in the field and prairie during fall and winter. In spring this reserve was rapidly depleted, water becoming nonavailable after May 1 in the field, but 1 to 10 weeks later in the prairie.

Discussion

Many changes occur when prairie sod is broken and the soil cultivated over a period of years. Water relations especially are greatly modified. Changes occur partly through the decrease in amount of living underground plant materials and content of organic matter. These are decreased because field crops are usually removed instead of being allowed to decay where they grow, and also because the underground materials of tilled crops are smaller in amount than those produced by prairie vegetation. Underground parts of little bluestem produce in the first 4 inches of soil 3.3 tons of dry matter per acre (Weaver and Harmon, '35). Mature winter wheat produced only about 12 per cent as much (.4 ton) underground materials on a similar upland soil (Kramer and Weaver, '36).

Fields under cultivation in Nebraska have lost from 6.5 to 28 per cent of their original organic matter. Where they had been subjected to cultivation for a period of 30 to 60 years, the maximum average loss was 56 per cent, and a loss of 27 per cent was determined on level, uneroded portions of the same fields (Russel, '29). Loss of organic matter is accompanied by the loss of nitrate nitrogen and moisture, as well as structure and tilth.

In semi-humid areas organic matter contributes to water conservation, especially in fields where the soil has sufficient clay to crack deeply upon drying. This results in great losses by surface evaporation. Organic matter reduces this tendency towards cracking. In the undisturbed prairie no surface cracks were formed at any time. Furthermore, organic matter by imparting stability to soil granules checks erosion either by wind or water. When highly erosive land is planted to grass both granulation and fibrousness of soil are increased, even far out of proportion to the organic matter added (Russel, '29).

The early plowing of the field afforded a soil condition favorable to the retention of moisture and resulted in a favorable condition for nitrate accumulation. This accounts for the excellent early growth of the crop. But nitrate production becomes insignificant at moisture contents as low as the hygroscopic coefficient. Consequently the wheat, and a little later the prairie, suffered a deficiency in both nitrogen supply and water.

Results of the runoff experiments are in accord with others that grassland absorbs much more water than cultivated fields (Miller and Krusekopf, '32; Conner *et al.*, '30). This usually does not occur when the showers are so light as to wet the loose field soil only to the depth of cultivation. But when larger amounts of rain fall the pores of the deeper soil become partially clogged by the fine surface soil particles carried downward in the percolating water. In undisturbed grassland, the plant cover and fallen litter protect the soil surface from the beating action of the rain. Water which runs off or percolates into the soil is not muddy but clear and the soil pores are not clogged with silt and clay (*cf.* Weaver and Noll, '35).

That the plants did not entirely succumb even when water was reduced to the nonavailable point to a depth of 4 feet resulted from their very deep rooting habits. A trench 9 feet in depth was dug in the wheat field on June 8 and the root systems examined. The soil was fairly moist between 4 and 9 feet in depth. Rather numerous wheat roots were found in the fifth and sixth foot, they were sparser at depths of 7 feet, but a few extended to 9 feet, despite the fact that the tops were only 18 inches tall. Numerous, relatively shallow-rooted prairie species wilted and died. Others, such as little blue-stem, with roots 4 to 5 feet in depth wilted and partly succumbed. The more deeply rooted species were able to remain alive although much injured (*cf.* Weaver, Stoddart, and Noll, '35).

RELATION BETWEEN PRECIPITATION AND PRODUCTION OF DRY MATTER

No relation between precipitation and the production of dry matter was found (table IV). There was no accumulation of soil moisture, except in the surface foot, either before or during the growing season. On the contrary there was a distinct decrease. Growth increased during periods of slight or no rainfall. Vegetation drew upon the small reserves of water available until they were exhausted. Then all plants except those that were very deeply rooted showed signs of distress.

The period of greatest production (67 per cent) in the prairie occurred in May. In June it decreased to 28 per cent. Thereafter there was a loss in amount of dry matter already produced. During a rather normal year of rainfall Flory ('36) found that 2 per cent of the total dry matter was produced in April, 26 in May, and a maximum of 36 per cent in June. July contributed 21 per cent and August 13. In the field, the greatest growth during 1934 occurred in May with a smaller amount in June. Only 10 per cent of the total growth occurred from October to April.

TABLE IV. *Monthly percentage production of dry matter and percentage of annual rainfall*

Criteria	March	April	May	June	July	August	Total
Dry matter, prairie	—	5	67	28	—51	—2	100
Dry matter, wheat	10 ¹	8	58	24 ²	—	—	100
Percentage rainfall	5	2	3	14	2	14	40

¹ This includes all dry weight made previous to March 1.

² Wheat harvested June 9.

Discussion

The prairie, except during drought, has moisture in excess of the demands of the dominants. Such marginal supplies account for the diversification of its structure. Subdominant species utilize these marginal supplies and make

possible the seasonal aspects. During 1934 the dominant species and many subdominants ceased growth after June 30. Only plants rooting at depths of 6 or more feet survived and flowered normally. Such species absorb water 6 to 18 feet below the soil surface. The available moisture in the fifth and sixth foot, and probably to 20 feet, while often only 2 to 3 per cent, was reduced less than 0.5 per cent during 1934 (*cf.* Weaver, '19).

The wheat plant requires an abundance of moisture at the heading stage. Good supplies of water in the boot stage are of nearly equal importance (Smith, '20). Uniform development can take place only when the demands for moisture are met. Precipitation during the growing period of the wheat was only one-third of that of previous seasons. Wheat, normally about 40 inches tall, averaged only 18 inches in height. The early drought caused rapid maturity. Heading was nearly complete by May 22. Many spikes scarcely extended beyond the leaf sheath. The grain dried on June 9, before it could ripen. The kernels, where present, were greatly undersize and much shrunken. Normally, wheat would have ripened three weeks later.

AERIAL CONDITIONS

Atmospheric environment deviated widely from the normal. Temperatures were abnormally high, humidity correspondingly low, wind movement unusually great, and evaporation extreme.

Temperature

Wheat continued growth as long as air temperature remained above freezing. At favorable temperatures the chemical processes of cell division were accelerated with the increased manufacture of food materials. Tillering increased, and gains were made in the number and size of leaves (*cf.* Weaver, Kramer, and Reed, '24).

Temperature and humidity were measured five inches above the soil by means of Friez' hygrothermographs housed and operated in the usual manner. The day period from October 1 to April 30 extended from 8 A.M. to 6 P.M. except that from December 1 to February 15, when 4 P.M. was used as the last day reading. From May to September the day included the 6 A.M. and 8 P.M. readings also.

Cover has a pronounced effect in modifying air temperatures near the surface of the soil. The prairie had been mowed in August, '33, at a height of 2.5 inches. A moderate growth of grass 4 inches tall had developed before the killing frost of October 22. The wheat had made a good autumnal growth attaining a uniform height of 4 to 5 inches.

The highest average weekly day temperature of the autumnal growing season was 66° F. in the field and 63° in prairie. The average maximum for the same week in late October was 76° in the field and the average minimum 46.5°. The lowest temperature recorded during the entire winter was 5°.

Temperatures during the mild winter were seldom critical for wheat. The plants remained green and probably grew intermittently. The average weekly day temperatures in the field varied between 25° and 46° F. and were nearly the same in prairie. The average daily maximum was 54° in both habitats. Average night temperatures ranged between 16° and 39° in the field, and 5° lower to 14° higher in the prairie. The lowest average minimum for any week was 13° in both habitats.

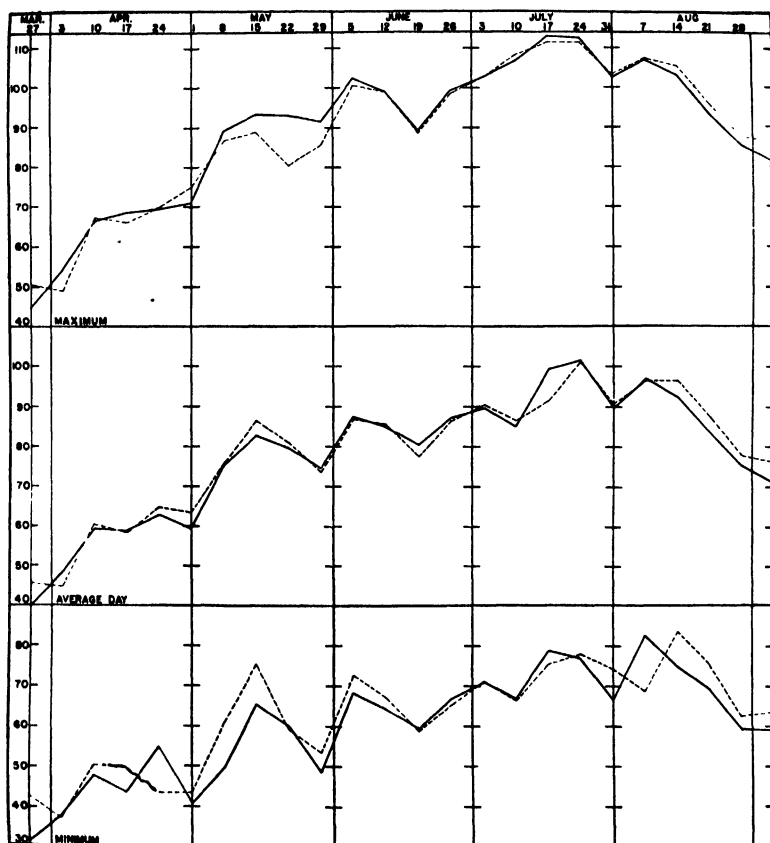


FIG. 6. Average air temperature by weeks in field (solid line) and prairie (broken line) from March 27 to September 4, '34.

During April temperatures rose rapidly (fig. 6). Until harvest on June 9, the average day temperatures in the field ranged from 40° to 88° F. Those in the prairie were from 3° less to 5° higher. A maximum weekly average of 102° in the field and 100° in the prairie was recorded during the first week in June. The highest temperatures for single days were 110° and 106° in the field and prairie, respectively.

After harvest, temperatures continued to rise until late in July when an

average day temperature of 102° F. was recorded in both habitats on July 24. Average maximum temperatures of 113° in the field and 112° in the prairie were also attained (fig. 6). During June and July the average minimum night temperatures ranged from 62° to 81° in the field and from 59° to 78° in the prairie. Temperatures gradually decreased during August.

Summarizing, average day temperatures during winter in the mowed prairie varied 16° F. and average night temperatures 19° more widely than those in the field. Average day maximum temperatures were the same in both habitats as were also the lowest average minimum temperatures recorded for any week. The prairie showed an 8° greater range in average day temperatures than the field until the time of harvest, but average maximum temperatures were 2° higher in the field. After harvest, the extremely high average maximum temperature of 113° was determined. Even the average night temperatures ranged as high as 81° in the field but 3° lower in the prairie. In general the growth of wheat produced in fall and winter afforded a better cover and stabilized temperature changes somewhat more effectively than did the mowed prairie with its scanty autumnal growth. Such extreme temperatures coupled with severe drought constituted the greatest catastrophe met by the vegetation of Nebraska within the memory of man. The wheat crop was a failure, the growth of prairie hay was too scanty to warrant mowing.

Humidity

The humidity of a plant's environment directly affects its rate of transpiration. The amount of water a plant loses frequently determines its ability to grow in a particular habitat. When humidity was low transpiration was high and plants suffered from excessive wilting.

During the autumn and early winter, average day humidity by weeks ranged from 48 to 81 per cent in the field and from 38 to 85 per cent in prairie. It was exceedingly low during the spring and summer. Before harvest the average day humidity ranged between 29 and 57 per cent in the field and was the same, or varied from 6 per cent less to 7 per cent more, in the prairie (fig. 7). The highest average maximum was 70 per cent in the field and 80 per cent in prairie. The minimum range was between 17 and 50 per cent in the field and 20 and 46 per cent in prairie.

After harvest the daily average humidity ranged between 20 and 48 per cent in the field and that of the prairie was the same to 8 per cent higher. The maximum never exceeded 72 per cent in the field nor 82 per cent in the prairie. The average weekly minima were often below 20 per cent in both habitats, and ranged between 12 and 37 per cent in the field. With a single exception, it was 1 to 3 per cent higher in the prairie. On certain afternoons humidity decreased to 5 per cent and once to 3 per cent.

Night humidity was also low. Humidity for the entire growing season was 8 per cent higher in the prairie and the maximum was 11 per cent higher. The average in the field ranged between 31 and 78 per cent.

Summarizing, winter humidities in the field and prairie were similar and not extremely low. During the hot spring and summer humidity was very low, often being 5 or more per cent higher in the prairie, especially after the

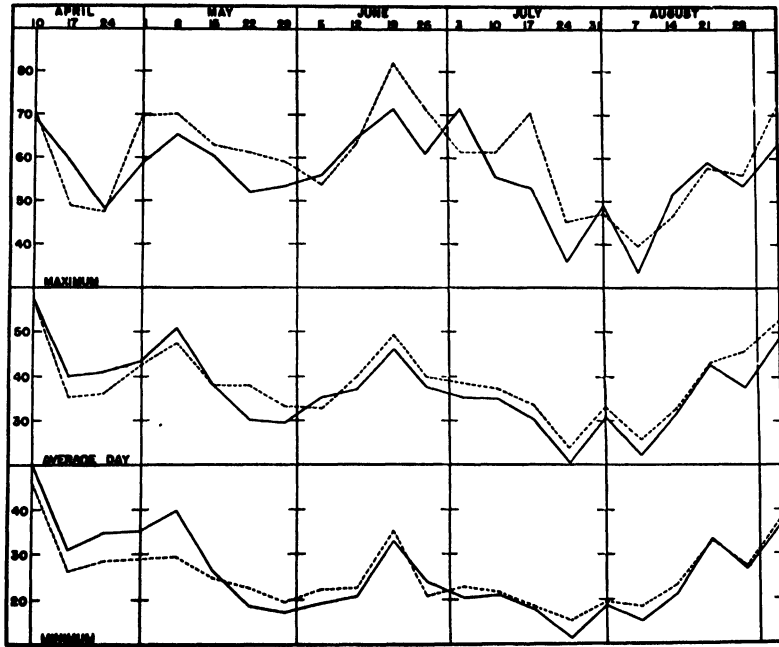


FIG. 7. Average relative humidity by weeks in field (solid line) and prairie (broken line) from April 10 to September 4, '34.

wheat began to dry. The minimum was 3 to 4 per cent higher in prairie. The extremely low humidities of July and August were also slightly less severe in the prairie.

Wind

Wind has a great influence upon increasing transpiration (Martin and Clements, '35; Harder, '35). Conversely the ground cover has a marked influence upon the movement of air in the strata of vegetation. Anemometers of the standard Weather Bureau type were placed in each habitat with the cups 12 inches above the soil surface. They were operated from April 20 to September 4 and were read on alternate days. The graphs, however, are based on average weekly wind movement.

Weekly wind movement in the prairie ranged between 3.5 and 7.4 miles per hour until June 9 (fig. 8). In the field it was always less, varying from 1.5 to 5.8 miles per hour. This, of course, was due to the greater height of plants in the field. Here the average level of the fully grown plants was 18 inches but 5 to 6 inches in the prairie. After harvest, on June 9, hourly

wind movement averaged consistently .25 to 1 mile less, and was often 5 miles per hour less in the prairie, notwithstanding the poor development of the grasses.

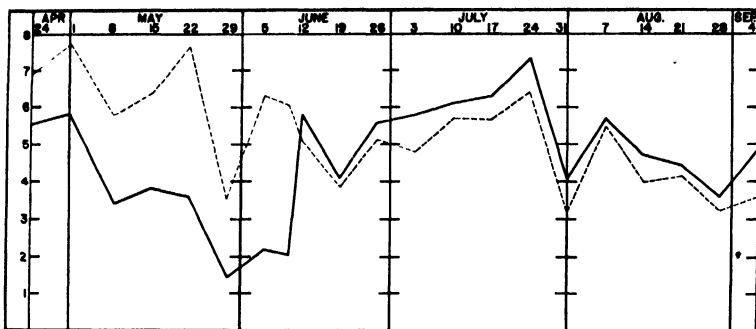


FIG. 8. Average daily wind movement by weeks in miles per hour in wheat field (solid line) and prairie (broken line) during '34.

Wind movement in the prairie was practically twice as great during the drought year as during any of the three preceding years, a difference due mostly to the dwarfed stature of the grasses (Flory, '36).

Evaporation

The rate of evaporation integrates in a general way the factors of humidity, wind movement, and temperature. Livingston's standardized, white, spherical, porous cup atmometers, fitted with non-absorbing devices, were used. They were operated in pairs at each station at a height of 4 inches. All readings were reduced to those of the standard atmometers (fig. 9).

Rates of evaporation were often twice and sometimes nearly three times as great as those recorded in the prairie during the three preceding years (Flory, '36). From May 22 to August 14 evaporation varied between 45 and 90 cc. per day. Before harvest, the rate of evaporation was consistently 3 to 20 cc. higher in prairie than in the field. Following harvest, it was 4 to 13 cc. higher in the wheat stubble than in the prairie. Evaporation rates in the field reached 85 to 89 cc. per day in July and August. During three separate weeks similar losses in the prairie were 72 and 82 cc. Even the minimum weekly losses during July and August were 62 cc. in the field and 40 cc. in the prairie.

SOIL TEMPERATURE

Temperature of the soil indicates in a general way the summation of the heat factors of the habitat. It combines the effects of direct insolation and radiation, and cooling by the evaporation of moisture. Soil temperature affects the rate of absorption of water and solutes as well as the activities of microorganisms (Bouyoucos, '13).

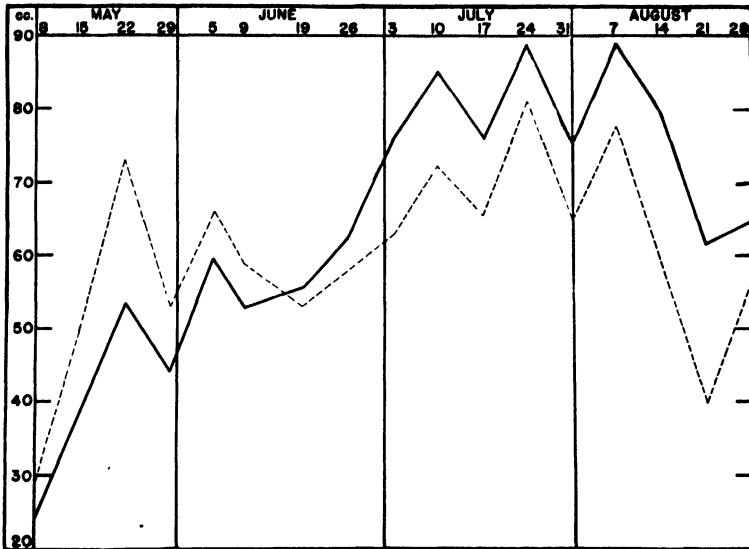


FIG. 9. Average daily evaporation by weeks in wheat field (solid line) and prairie (broken line) during '34.

Soil thermographs were used for securing a continuous record of the temperature at 3 inches depth. Thermometers were used for measuring surface and deeper soil temperatures. They were fastened to the ends of cylinders of hardwood of appropriate lengths and the bulbs inserted through corks into glycerin in pointed brass caps of 25 cc. capacity. Holes into which the cylinders fit were made with a geotome and the brass caps left in contact with the soil between weekly readings. Change in temperature of the glycerin was too slow to introduce an error in reading when the cylinders and thermometers were withdrawn. Temperatures were taken at depths of 3, 12, 24, 36, and 48 inches.

Temperature of fall and winter

Surface temperatures in prairie were higher until December 7 than those under the protecting wheat leaves in the field. During the winter they were the same or 2° to 4° F. lower. Surface soil in both field and prairie fell below freezing by mid-December but was consistently above after February 20. The minimum was 29°.

Temperatures at 3 inches depth showed that the prairie vegetation was a heat stabilizer. During a week late in February for example, the graph from the prairie was a straight line sloping from 31° to 30° F. That from the field varied from 32° to 29° with a daily fluctuation of 3°, a phenomenon due to the more exposed dark field soil. During the winter the average field temperature ranged from 40° to 29.6° and that of the prairie varied from 36.6° to 30°. The average minimum for the coldest week in January was 28.6° in the field and 29.6° in the prairie.

At the 12-inch depth, temperatures in the field during the winter were the same as in the prairie or 1° to 3° lower. The temperature was below freezing (minimum 30°) for only about twenty-one days.

Differences greater than 2° were not determined at the 2-foot depth during fall and winter. At greater depths differences were even smaller and neither habitat was consistently warmer nor colder. The lowest temperatures at 2, 3, and 4 feet were 35° , 38° , and 38.5° , respectively.

Temperatures of spring and summer

The surface field soil warmed in spring much more rapidly. Differences of 6° to 8° were common and those of 16° to 17° were determined. During the dry summer, the field soil (with one exception) remained continuously warmer. Differences in temperature varying between 4° and 17° were recorded (fig. 10).

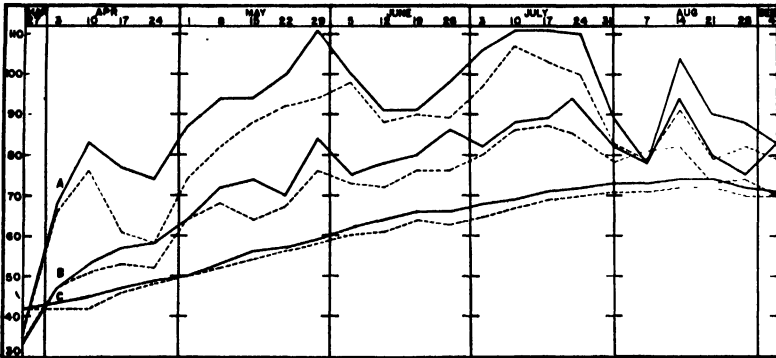


FIG. 10. Soil temperatures (10 A.M.) at the several depths in wheat field (solid line) and prairie (broken line) during spring and summer of '34. A, surface; B, 3 inches depth; C, 48 inches depth.

A general rise of temperature at 3 inches depth occurred from March to June. Average weekly day temperatures in the field were usually 2° to 10° F. higher than those in prairie. After harvest, temperatures in the field ranged from 72.6° to 95.7° ; those in prairie ranged from 73.6° to 92.8° . The average daily maximum temperatures were, in the same sequence, 79° to 106° and 77.1° to 96.4° . Maximum temperatures of 112° were recorded in the field and 104° in the prairie.

The prairie soil at 12 and 24 inches depth was nearly always 2° to 5° F. cooler than that of the field. At 3 feet, there was little difference until the first of June. Thereafter the field was 1° to 4° warmer, and at 4 feet 2° to 3° warmer than the prairie (fig. 10).

Differences in extremes of temperatures between winter and summer were greater in the field to a depth of 3 feet (table V).

TABLE V. *Differences between highest and lowest temperatures in degrees Fahrenheit in prairie and field*

Depth	Prairie			Field		
	High	Low	Difference	High	Low	Difference
Air 5 inches above surface	117°	-3°	120°	118°	-5°	123°
Surface	107	29	78	111	29	82
3 inches	87	30	57	94	29	65
12 inches	84	30	54	86	30	56
24 inches	79	36	43	82	35	47
36 inches	75	39	36	78	38	40
48 inches	72	38	34	74	40	34

Range in temperature decreased with depth. Soils undergo a complete reversal of temperature both in spring and fall (*cf.* McCulloch and Hayes, '23). The autumnal reversals in the field occurred October 17-24 but more than a week later in prairie. In spring it occurred in both habitats during April 7 to 14.

Discussion

The importance of extremes in environmental influences warrants their careful measurement and study. As pointed out by Taylor ('34), extreme conditions are probably more significant in appraising action of environment than are the more ordinary environmental relationships. The extremes of greatest importance in growth of crops and prairie in Nebraska are deficient moisture, excessively high temperatures, abnormally high winds, and excessive evaporation. Wheat is also frequently subjected to too low winter temperatures which do great damage.

LEAF AREA

Determinations of leaf area per square foot of soil were made at ten-day intervals during the growing season. A wire frame, one foot square, was used in delimiting the native grass or wheat to be cut. The vegetation from four separate square feet was taken at each sampling, different soil areas being used. The quadrats were selected from typical little-bluestem sod, which was practically free from forbs. Samples were also taken from typical areas of wheat. The frame was placed close to the ground and the vegetation growing within the area carefully separated from that without. It was then clipped at the soil surface, care being taken to secure all of the leaves.

The plants were cut in the early forenoon, care being taken to keep all cut ends downward, wrapped in soft, wet paper and taken to the laboratory. The bases of the bundles were placed in jars filled with water to a depth of an inch for several hours in order to insure turgidity and prevent shrinking and folding or rolling of leaves. The bundles were then unwrapped and their contents weighed. Leaves of the four samples were next thoroughly

mixed by rolling them lightly back and forth over wet paper. One-fourth, by weight, was selected as representative of a typical square foot sample.

Leaves of the selected sample were sorted into 4 to 6 groups depending upon their length. Ten leaves were selected at random from each group and solio prints made. The areas were determined by means of a planimeter. The average area of each group was multiplied by the total number of leaves in the group. The total area was then multiplied by two, since both sides of the leaves received light and transpired. The product gave the total leaf surface, in square inches, from one square foot of soil.

Andropogon scoparius constituted 60 to 70 per cent of the entire prairie vegetation, and in selected areas as well as in the phytometers over 85 per cent. Therefore this type was used as representative of the plant cover. Intermixed with it were small amounts of other grasses of somewhat earlier growth which increased the total area.

Leaf area per square foot was 96.8 square inches on April 24 (table VI). It gradually increased to a maximum of 350.3 square inches by May 15. Twelve days later, as a result of the drought, the leaf surface decreased to 316 square inches, the leaves having withered and dried at the tips. Ordinarily maximum growth is not attained until about July 15. The decrease was marked day by day until on July 14 the area was only 16.4 square inches. After this most of the foliage became dry and discolored and no further growth occurred.

TABLE VI. *Leaf area in square inches per square foot of soil, and height of vegetation in inches*

Criteria	Mar. 6	Mar. 22	Apr. 10	Apr. 24	May 5	May 15	May 27	June 5	June 18	June 30	July 14
Leaf area, grasses	—	—	—	96.8	252.4	350.3	316.0	283.7	184.8	121.5	16.4
Height, little bluestem	—	—	—	2	—	—	5	—	—	6	6
Leaf area, wheat	199.7	200.7	316.3	477.7	531.5	174.8	76.8	8.0	—	—	—
Height, wheat	—	3	—	9	—	—	18	18	—	—	—

When the wheat renewed growth in spring, only the distal half of the leaves had been killed. This excellent survival resulted from the mild winter. On March 6, three days after the melting of a late February snow, the leaf area was 199.7 square inches per unit area of soil. No increase occurred until after March 22. The maximum area, attained on May 5, was 531.5 square inches. Thereafter the lower leaves dried and shriveled more rapidly than new ones were produced. Due to dry weather and the early ripening of the grain, leaf area decreased rapidly until it was only 8 square inches per square foot of soil on June 5, four days before harvest. Instead of ripening normally, the crop dried as soil moisture was depleted.

PHYTOMETERS

Phytometers were used to measure water losses through transpiration and surface soil evaporation. The prairie phytometers were cylindrical, one-half square foot in cross-sectional area, and 30 inches deep. They were made

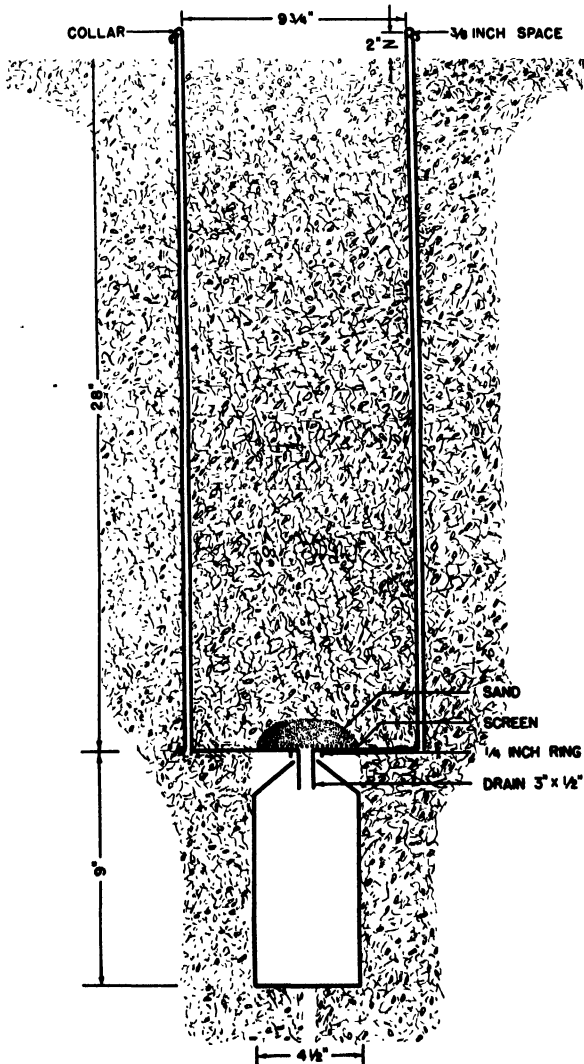


FIG. 11. Vertical section of phytometer used in prairie to determine loss of water by transpiration and surface evaporation.

of No. 22 gauge galvanized iron, and were filled with surface prairie soil, which was tamped firmly, to a depth of 20 inches. Cores of little-bluestem sod 8 inches deep and just large enough to fit tightly into the phytometers

were taken from the prairie and pressed firmly into place. They filled the containers to within 2 inches of their tops. Six such phytometers were placed in holes 28 inches deep and three-fourths inch larger in diameter than the phytometers. Each hole was lined with a galvanized iron cylinder which extended 2 inches above the soil surface to prevent any water from running in. The holes were in a straight row and spaced 8 inches apart. The soil surface in the phytometers was thus on the same level as the surface of the prairie. Details of construction and provision to recover percolated water are shown in figure 11 (*cf.* Fredricksen, '38).

The phytometers were weighed once each month in winter (except during February) and at 10- to 16-day intervals in summer by means of a portable platform balance sensitive to $\frac{1}{16}$ pound. The framework to hold a portable platform used during weighing is shown in figure 12.

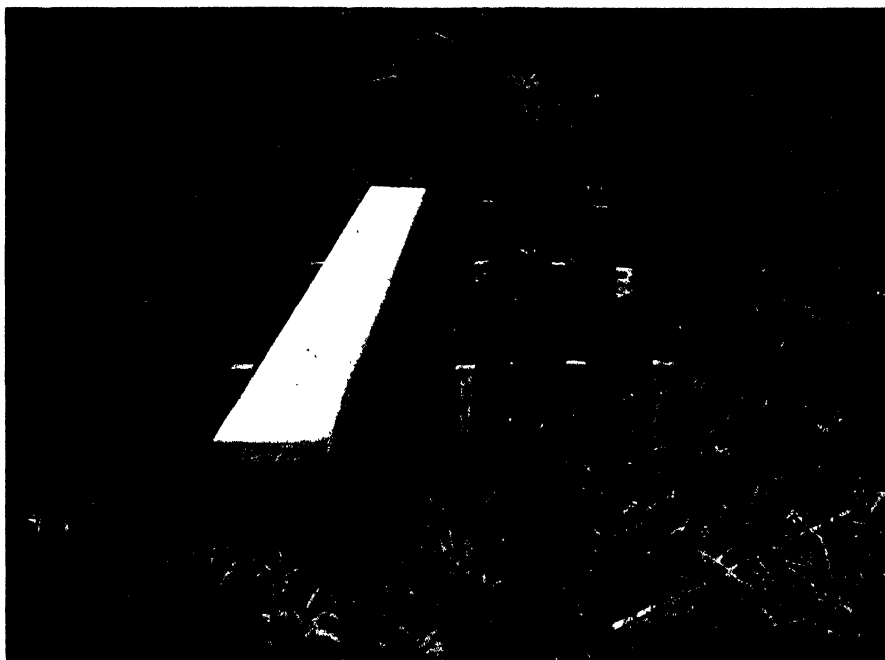


FIG. 12. Method of weighing prairie phytometers without disturbing the surrounding vegetation. Two of the phytometers are partly elevated in the row between the stakes which support the platform; only one of the three planks that support the balance is in place. Photo. in early summer.

Wheat phytometers were 9 inches square and 32 inches deep. They were filled with surface soil to within 2 inches of the top. The wheat was sown in two rows 7 inches apart in each phytometer so as to simulate field conditions.

Ten wheat phytometers were placed in a trench in the field. The trench

was 10 feet long and 20 inches wide, with two right-angled projections of similar width (fig. 13). The trench was walled and floored with two-inch planks. It was covered with a hinged roof except the part holding the phytometers. These were placed in one end of the trench, two containers of wheat being used as buffers. Thus, as in the prairie, the experimental crop was entirely surrounded by an undisturbed crop of its kind.

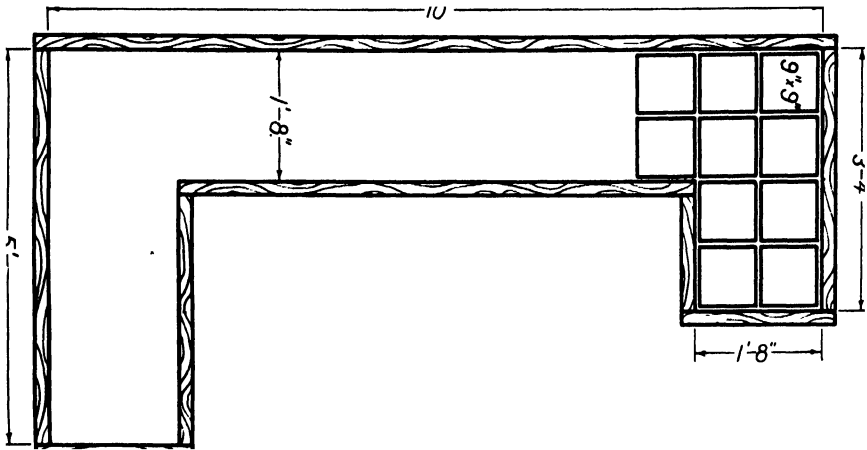


FIG. 13. Top view of trench in field entirely surrounded by wheat, showing the arrangement of the 8 wheat phytometers and the 2 buffer containers. The hinged doors of the remainder of the trench, used for weighing, are not shown.

In weighing, the roof was opened at right angles, revealing the small platform balance in the corner of the main trench. The phytometers were weighed in order, temporarily placed in the vacant right-angled projection of the main trench until all weights were recorded, and then returned to their original position. Thus there was no trampling or other disturbance of the surrounding crop.

WATER LOSSES AND PRODUCTION OF DRY MATTER

The water losses are not entirely representative of the natural prairie and wheat field, since some water was added either at the time of weighing or occasionally at intervening periods. This was done partly to compensate the limited depth of soil (30 inches) in the phytometers and partly to keep the plants therein from premature wilting. Hence, by the addition of the amounts of water shown in table VII the prairie vegetation was kept from wilting but the growth afforded only the scanty yield of a dry year. The wheat was kept green until the stalks were 24 inches tall instead of 18 and the dwarfed heads fairly well filled.

TABLE VII. *Pounds of water added to phytometers*

Station	April		May			June		July		August		Total
	12	27	10	20	30	11	25	7	21	4	18	
Wheat	—	3	8	10	10	—	—	—	—	—	—	31
Prairie	2	2	5	4	6	4	7	6	12	4	6	58

Marked differences were found in the water loss in wheat field and prairie. During fall and early winter when the wheat was becoming established the water losses were slightly less in the field than in the native grassland. They varied from .18 to .33 pound per square foot per day but were .22 to .36 pound in the prairie (fig. 14).

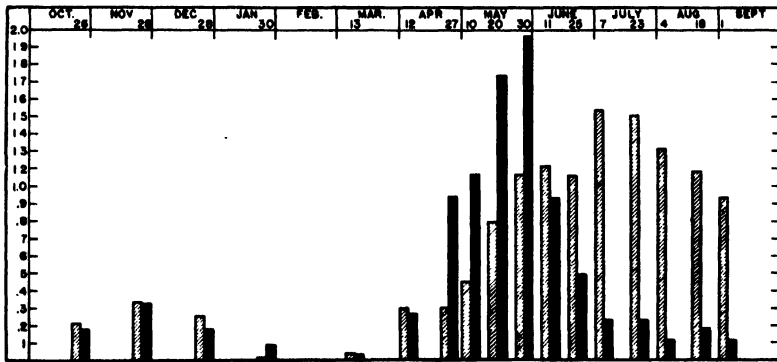


FIG. 14. Average water loss in pounds per day per square foot of soil from phytometers in wheat field (black) and prairie (hatched). The wheat was cut on June 9, '34.

During the winter, dormancy was more complete in the prairie than in the field, where the plants remained green even after the leaves were frozen. Losses during mid-winter when the soil was usually frozen were very small; the maximum was .09 pound.

During the last half of March and early April losses in the field and prairie were almost equal. Thereafter until harvest they were 2 to 2.4 times greater in the field. The greatest losses occurred late in May, 1.97 pounds in the field and 1.17 pounds in the prairie.

Two days after the wheat was harvested (June 11) the average daily water loss was only .93 pound in the field and 1.22 pounds in the prairie. Thereafter they were very much higher in prairie than in the stubble field, the soil being so dry that there was no development of weeds. The maximum in prairie occurred during June 27 to July 7 when 1.54 pounds per day were lost. Water losses till July 23 were nearly as great. But those in the stubble for the two periods were only .46 pound. Thereafter transpiration-evaporation rate decreased as both vegetation and soil dried (fig. 14).

The water loss through transpiration and evaporation during this season of drought was extremely great in comparison with the amount of dry matter produced. Losses were 10 to 20 times higher than during any of the three preceding years (Flory, '36). The water used or evaporated from the soil in producing a pound of dry matter of wheat (September 30 to June 9) was 2,400 pounds. That used by prairie vegetation (April 12 to September 1) was 5,584 pounds. Fredricksen ('38) determined that 1,296 pounds of water were used by phytometers in prairie in the production of one pound of dry matter during the rather favorable growing season of '35, but 2,684 pounds during the drought year of '36.

The water lost from phytometers in the wheat field from September 30 to March 13 was 3.5 tons per acre per day and that from the prairie was 4.2 tons. Losses from March 13 to June 11 were 20.8 tons in the field and 13.3 tons in the prairie. After harvest the loss was less, 5.1 tons in the field, but it was greater in the prairie, 27.8 tons, from June 11 to September 1.

DISCUSSION

Growth of foliage is a reliable index of the favorableness of climatic conditions. The leaves receive the full impact of the aerial environment and their activities determine the size of the plant. Although the mature wheat plant may develop under drought as many leaves per stalk as under conditions favorable for growth, yet the leaves are reduced in length, width, and area for photosynthesis. Moreover, their structure is profoundly modified. In the mixed crops—grasses, legumes, mints, composites, etc., of prairie, which develop and ripen often at widely different times during the growing season—some are more likely to escape unfavorable conditions than is a single species as wheat where all of the plants ripen at the same time. Conditions during '34, however, were so severe as greatly to retard development of all but plants of very early spring, except those rooted very deeply below the zone of effective soil drought.

Weaver and Crist ('24) obtained an average daily loss of .85 pound of water per square foot from upland prairie vegetation during a period of 15 days (July 24 to August 8, '23). Their results, however, were obtained during a year of heavy rainfall, high humidity, and low temperatures. The approximate sunshine during the experimental period was only 47 per cent, the average day temperature 79° F., and the average daily humidity 80 per cent. Hence it is easy to understand why losses nearly twice as great (1.54 pounds) were obtained even from a scanty vegetation under the extremely dry and hot weather during '34.

In prairie vegetation, the plant cover is adjusted to a normal water supply. It may increase gradually over a period of wet years, but decreases again, even below the mean, during continued dry periods. Climax vegetation yields slowly to the effects of extreme conditions. It is usually able slowly to recover

its former state upon a return of normal environment. Wheat, on the contrary, quickly develops a luxuriant top in response to an abundant water supply. If drought occurs early it may be greatly harmed and never fully recover. Conversely, if early conditions for growth are very unfavorable, it cannot compensate late in life even if moisture is abundant.

Many climatological factors are responsible for the development of vegetation. Each year presents these factors in varying combinations. Native vegetation integrates the factors and indicates by its growth the intensity of the favorable or unfavorable combinations. When a good cover of plants is developed it has a marked effect upon stabilizing water-content, temperature, humidity, wind movement and many other habitat factors. But when it is sparse the soil is less protected from the drying influence of direct insolation, and all of the factors are more extreme (Weaver and Flory, '34).

SUMMARY

Studies in upland, climax prairie and an adjacent field of winter wheat were made at Lincoln, Nebraska, from September, '33 to September, '34.

The growing season was the driest and hottest ever recorded. Precipitation was below normal every month except December. Only 10.49 inches of the mean precipitation (24.27 inches) of the eleven months occurred.

Runoff from the Carrington silt loam to the amount of 1.2 per cent of the rainfall occurred in prairie, and 8.7 per cent in the field, mostly after harvest.

The winter water supply of 10 to 20 per cent at 4 to 24 inches depth was entirely exhausted in June (4 to 12 inches) or July (12 to 24 inches) and was not replenished. About 8 per cent occurred in the third and fourth foot during fall and winter. Here water became nonavailable in prairie in July, a slight residue remaining in the fourth foot of field soil.

Available water content was usually several per cent higher in prairie to a depth of 2 feet, but slightly lower than in the field in the third and fourth foot. The field soil cracked deeply. Below 4 feet, water was continuously available in small amounts.

Vegetation was dependent largely on the water reserves in the soil, hence no relation was found between precipitation and production of dry matter. Prairie produced 67 per cent of its dry matter in May and the field 58 per cent.

Plants of shallow root extent died; those of moderate depths suffered greatly; and only deeply rooted species functioned normally. The dwarfed wheat plants dried early in June before the half-filled kernels could ripen.

Wheat afforded a better cover and stabilized temperature changes during winter more effectively than did mowed prairie.

Maximum weekly average temperatures of 100° and 102° F. were recorded in prairie and field, respectively, during the first week in June, and 113° at both stations in July.

During the hot spring and summer, average weekly humidity minima of

20 per cent or less occurred. Humidity was higher in the field until the wheat dried; thereafter it was usually 5 or more per cent higher in the prairie.

Wind movement was 3 to 7 miles per hour. Before harvest it was 2 to 2.4 miles per hour greater in prairie, thereafter .25 to 5 miles per hour greater in the field.

Evaporation during a period of 84 days ranged from 42 to 90 cc. per day. Before harvest it was 3 to 20 cc. per day greater in prairie, thereafter 4 to 13 cc. greater in the field.

Maximum surface soil temperatures, at 10 A.M., of 107° and 111° F. were recorded in prairie and field, respectively. Maximum soil temperatures of 104° were recorded in the prairie in July, and 112° in the field at 3 inches depth. Winter-summer extremes of temperature were greater in the field to a depth of 3 feet.

Water losses per square foot per day from phytometers were, after April 1, 2 to 2.5 times greater in the field, where a maximum of 1.97 pounds was reached.

Maximum leaf areas per square foot of soil were attained in May; they were 350 square inches in prairie and 531 in the field. Leaf areas were early reduced by rolling and folding, and later by drying and death.

Water used by vegetation while producing a pound of dry matter was 2,400 pounds in wheat field and 5,584 pounds in prairie.

Water losses from March 13 to June 11, calculated from weighed phytometers, were 20.8 tons per acre per day in the field and 13.3 tons in the prairie.

The writer wishes to acknowledge his indebtedness to Dr. J. E. Weaver for outlining the problem and for direction and encouragement throughout the course of the work.

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BACKGROUND SELECTION IN CRAYFISHES

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Many papers have been published during the past few years upon the subject of color changes in animals and the extent to which animals are able to simulate the color, shade, and pattern of the background; but astonishingly little has been learned about any corresponding adaptive background choice in animals that are able to so change their coloration. It is interesting to learn whether animals that are once adapted to a particular shade of background tend to select a background of the same shade to any extent. The works of early investigators of the color adaptations in crustaceans suggested that there was such an adaptive background choice. Keeble and Gamble ('04) gave some data upon this problem for crustaceans. Summer ('11) and Mast ('16) gave conflicting statements for adaptive background selection in fishes. Brown and Thompson ('37) made a survey of background selection in a number of small freshwater fishes and found that such a selection was modified along with skin coloration of the animal as it was determined by background. Different fishes showed different degrees of this modification.

Crayfishes show a limited amount of color adaptive ability. These experiments were performed to determine whether they, like fishes, have their background choice modified along with color adaptation. Furthermore, it seemed interesting to learn to what extent background selection was a phenomenon distinct from phototropism in its simplest sense. In other words, do crayfishes select one background over another solely as a function of the extent of asymmetrical stimulation of the two eyes or is there some degree of specialization of the response mechanism for the process? The following experiments have given some answers to these questions.

EXPERIMENTAL

The crayfish, *Cambarus immunis* Hagen, was used in all the following experiments. The specimens were small, ranging in carapace length from 16 to 32 mm.

The inner surface of a shallow pan, $31 \times 38 \times 6$ cm., was painted in such a way that one half the bottom with the adjacent wall was painted black and the other half and walls, white. The line of junction between the white and black halves was in the direction of the longest dimension of the pan. This was called the "choice pan" in accordance with the terminology used by Brown and Thompson ('37). Set inside of the choice pan was a second pan,

the general shape of which resembled a section through a funnel in the long axis of the stem. This second pan, the "adaptation pan," was either black or white internally depending upon the particular experiment. The adaptation pan could be set into the choice pan in such manners that the animal emerging through the open stem would make a right or left choice to black or white, could encounter black on both right and left, or white on both right and left. Figure 1 (*A, B, C, D*) indicates the positions of the adaptation pan in the

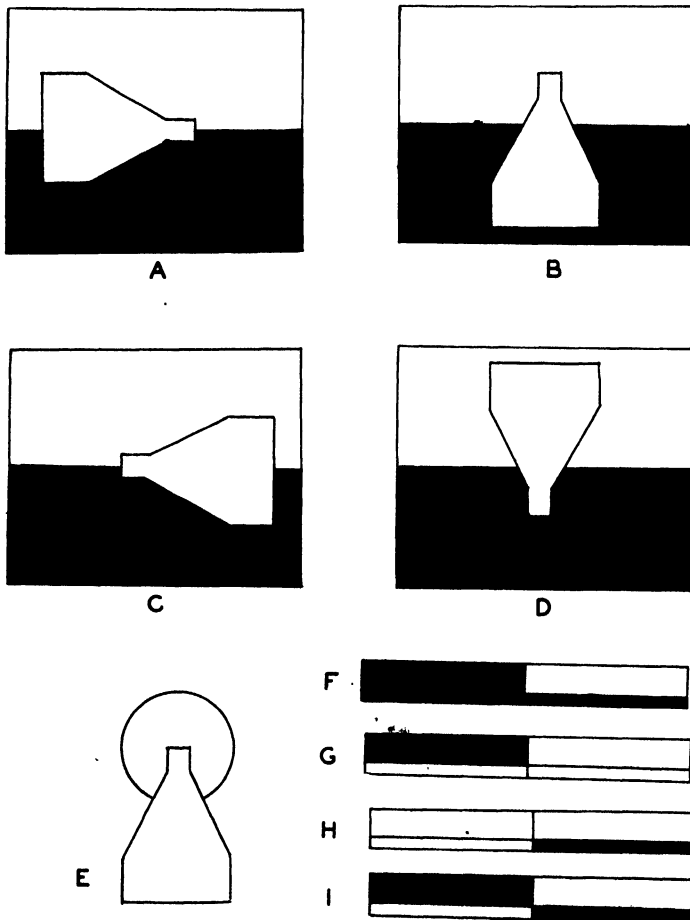


FIG. 1. *A-D*: Diagrams showing the various positions of the adaptation pan in the choice pan used in the accompanying experiments. *E*: The arrangement of a circular enclosure about the stem of the adaptation pan used to produce differential stimulation of the upper and lower halves of the eyes. *F-I*: The distribution of black and white paint on the inside of the circular rings used to produce the various experimental combinations.

choice pan that were used in the described experiments. Diagrams 1*B* and 1*D* show instances when the right and left choices on emergence yielded the

same color of background, while diagrams 1A and 1C show arrangements in which the right or left choice was one of black on the one side and white on the other.

Five inside faces of a cuboidal box 50 cm. on an edge were painted. The remaining side, that facing the observer, was left open. The box was painted so that one side and half the adjacent top, bottom, and end was painted black, while the remaining half of the box was white. The end was interchangeable so that the box could be turned end for end and the side that was at the observer's right could be black or white. Thus, in all the experiments, there was adequate control for any tendencies of right- or left-handedness that might occur in the crayfishes.

The choice pan was placed in the box so that the line of junction between its black and white halves corresponded with the junction upon the bottom of the box, or, so that the adaptation pan stem was opposite the junction of the black and white of the box in those instances in which the stem of the adaptation pan opened to a right and left choice of the same shade of underground.

A 40 watt daylight incandescent lamp projected through the top of the box exactly in its center, and at the line of junction of the black and white of this top. The illumination at the center of the choice pan surface was about 22 f.c.

It is obvious that an animal emerging from the stem of the adaptation pan would have all those ommatidia directed at an angle of less than about 41° above the horizontal stimulated by the corresponding side of the choice pan due to the internal reflection of the water surface working in conjunction with light reflected directly from the background. A slight modification of the apparatus was made in order to obtain situations in which only the ommatidia directed below the horizontal were stimulated by the choice of pan background. This last was accomplished by bending strips of sheet iron, 5.5 cm. wide, into nearly complete rings and fitting them over the stem of the adaptation pan in such a way that the crayfish, upon emerging, would find itself in the center of a circular enclosure, 15 cm. in diameter (see figure 1E). The insides of the strips were painted differentially on the right and left halves with black and white paint so that (with the choice pan filled with water to a depth of 5.5 cm., and even considering the internal reflection of the water) the upper and lower halves of the crayfish retina could be stimulated differently and independently in the two eyes of the animals (see figures 1F, 1G, 1H, 1I).

With this apparatus it was possible to stimulate various portions of the retina of the crayfishes with light reflected from the black and white asymmetrically in the two eyes and determine the effects in the orientation of the body.¹ The experiments in which the stimulation was to be equal in the upper ommatidia (those directed at an angle greater than 41° above the horizontal)





¹ In all the experiments, a small solid sector in the upper posterior portion of the eyes was symmetrically stimulated as a result of the absence of a wall on the box on the side towards the observer. Later work showed this to be relatively insignificant in effect.

TABLES 1 AND 2. The diagram heading each table is a schematic representation of the two eyes of a crayfish in dorso-ventral section, and indicates roughly the portions of the two eyes stimulated by white (unshaded) and black (shaded) background reflected light. Beneath each diagram are shown the numbers of choices out of each 50-animal series that the crayfishes turned in the direction of one or another retinal stimulus pattern.

Exp.	Table 1 (White adapted)		Table 2	
	L.	R.	L.	R.
1	28	22	37	13
2	29	21	35	15
3	30	20	38	12
4	31	19	49	1
5	39	11	43	1
6	35	15	49	1
7	48	2	44	6
8	48	2	45	5
9	38	12	32	18
10	45	5	44	6
11	49	1	46	4
12	46	4	47	3
13	50	0	35	15
14	50	0	41	9
15	49	1	49	1
16	40	10	43	7
17	36	14	50	0
18	46	4	50	0
19	38	12	37	13
20	43	7	38	12
21	42	8	38	12
22	25	25	39	11
23	30	20		
24	35	15		
25	40	10		
26	39	11		
27	40	10		
28	41	9		
Av.		10.4		7.5
Standard error		± 1.3		± 1.2

were performed outside of the above described box with the pan symmetrically placed before a window and the sides approximately equally illuminated by the diffuse light from the white walls and the ceiling of the room. In order to make for greater similarity between the experiments performed inside and





TABLES 3, 4, 5, AND 6. See legend for tables 1 and 2

	Table 3		Table 4		Table 5		Table 6	
								
Exp.	L.	R.	L.	R.	L.	R.	L.	R.
1	42	8	37	13	36	14	20	30
2	44	6	34	16	37	13	21	29
3	47	3	38	12	33	17	17	33
4	45	5	28	22	29	21	31	19
5	39	11	33	17	28	22	31	19
6	44	6	30	20	24	26	31	19
7	46	4	36	14	33	17	30	20
8	41	9	38	12	23	27	28	22
9	42	8	36	14	35	15	39	20
10	44	6	36	14	32	18	30	20
11	40	10	35	15	17	33	20	30
12	39	11	41	9	33	17	18	32
13	47	3	37	13	29	21	31	19
14	47	3	38	12	33	17	23	27
15	26	24	47	3	26	24	27	23
16	36	14	36	14	22	28	23	27
17	50	0	38	12	20	30	38	12
18	50	0	29	21	28	22	21	29
19	50	0	29	21	34	16	21	29
20	45	5	25	25	35	15	24	26
21	39	11	32	18	36	14	27	23
22	49	1	33	17	35	15	18	32
23	39	11	25	25	31	19	34	16
24			49	1			25	25
25			41	9			16	34
26			49	1			19	31
27							19	31
28							25	25
29							24	26
30							24	26
31							21	29
32							14	36
33							17	33
34							18	32
35							30	20
36							34	16
Av.		6.9		14.3		20.0		25.5
Standard error		± 1.1		± 1.2		± 1.1		± 1.0

outside of the box, a light was suspended about 50 cm. directly over the center of the apparatus in the latter experiments. The illumination at the level of the choice pan in these experiments varied from 70 to 200 f.c.

For any given experiment the apparatus was so adjusted as to stimulate the eyes of the crayfish emerging from the stem of the adaptation pan in the particular manner desired. Fifty crayfishes were then taken from a situation of background adaptation, black or white, depending upon the experiment, and run through the stem of the adaptation pan one at a time. The number of

TABLES 7, 8, 9, AND 10. *See legends for tables 1 and 2*

	Table 7		Table 8		Table 9		Table 10	
								
Exp.	L.	R.	L.	R.	L.	R.	L.	R.
1	41	9	32	18	44	6	34	16
2	43	7	14	36	33	17	33	17
3	41	9	27	23	35	15	31	19
4	38	12	32	18	38	12	32	18
5	45	5	26	24	36	14	32	18
6	41	9	25	25	30	20	30	20
7	43	7	24	26	34	16	31	19
8	43	7	23	27	30	20	34	16
9	49	1	30	20	36	14	37	13
10	33	17	29	21	35	15	36	14
11	43	7	36	14	31	19	35	15
12	46	4	28	22	38	12	48	2
13	42	8	8	42	32	18	47	3
14	46	4	29	21	36	14	44	6
15	36	14	26	24	24	26	46	4
16	40	10	19	31	31	19	39	11
17	50	0	29	21	31	19	36	14
18	46	4	23	27	48	2		
19			33	17	44	6		
20			28	22	43	7		
21			27	23	45	5		
22			32	18	30	20		
23					29	21		
Av.		7.4		23.6		14.6		13.2
Standard error		± 1.0		± 1.2		± 1.2		± 1.4

choices to one side or the other was recorded. In one of the experiments the crayfishes were white adapted and permitted to emerge from a white adaptation pan. In all the others, the animals were always black adapted and a black adaptation pan was used.

An animal was considered to have made a choice when one eye crossed a line drawn parallel to an imaginary line longitudinally bisecting the stem of the adaptation pan and 2.5 cm. away.

The accompanying tables, with their diagrams, are more or less self-explanatory. The circle diagrammatically represents the two eye surfaces of the animal in dorso-ventral section, the vertical line through the center separating the one eye calotte from the other. That part of the eye shaded indicates the portion of the eye that was stimulated by black background reflected light; the unshaded part shows that portion stimulated by light from a white background. Beneath each diagram are given a number of trials, 50 animals

each, for the situation in question and the number of choices made in each direction. In each case the averages have been calculated and the standard errors of the averages determined. The number of individual choices for the experimental situations are seen to vary from 850 to 1800. This number of trials, together with the small standard error, indicates the validity of the results that have been obtained.

DISCUSSION OF RESULTS

Tables 1 and 2 show the results of experiments in which the only variable has been the background adaptation. Those crayfishes that were white adapted and emerged from a white adaptation pan tended, on the average, to select white a little more frequently than animals that were black adapted and emerged from a black adaptation pan. Examination of the standard errors, however, make one a little doubtful of the significance of the difference between the average responses in these two lots of animals. In the light of the positive results with fishes that were obtained by Brown and Thompson ('37), these results with crayfishes may be indicative.

Now, examining tables 2, 3, and 4, and also tables 8 and 9, one is immediately impressed with the fact that the strength of the orienting force is a function of the relative amounts of the retina stimulated by black in contrast with white background reflected light.² This relationship is depicted, in the light of all the available data, in figure 2. This figure shows this relationship to be a sigmoid one. That is, if we start with a situation in which the two eyes of the crayfish are symmetrically and uniformly stimulated by white background reflected light, then start with the upper or lower limit of the eye and stimulate greater and greater fractions of one eye with light from a black background, we find the effectiveness of the asymmetrical stimulation increases as we cover larger areas towards the onmatidia directed horizontally and then gradually decreases toward the periphery of the eye on the opposite side. This is merely another way of stating that the upper and lower extremes of each eye are relatively ineffective in determining the orientation of the animal to background as compared with the upper and lower more central portions. This is seen in comparing tables 2 and 3 where in spite of the fact that a number more onmatidia are stimulated by black in 3 than in 2, yet there is not a significant difference between the means of the two responses. Again in table 6, though the two eyes are asymmetrically stimulated with respect to the upper few onmatidia, yet the average response is

² The white and black grounds, of course, yield only different percentages of light reflected, and permit a relatively normal ratio of strengths of simultaneous stimuli which strike the eyes of the creeping crayfish. The same results could be expected were light directed into the eyes at the same angles from luminous sources of various brightness and the ratio of the differences in two eye portions could in this latter instance be made abnormally high or low. The source of stimuli used in this research seemed more natural as well as convenient to produce the differential stimulation.

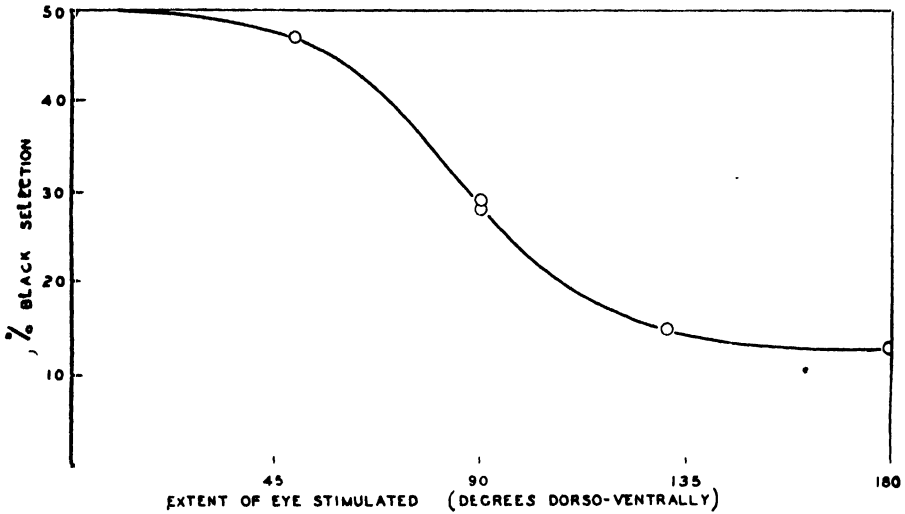


FIG. 2. The relationship between the amount of one eye stimulated by light from a black background and the percentage of movement onto the black surface. The area thus "seeing black" is always continuous with the upper or lower edge of the eye.

not different from the random 50-50 distribution. Similarly, table 7 does not show a significant difference from table 2, nor table 8 from a random 50-50 distribution. The data of tables 3, 6, and 7 are subject to an explanation to be considered later.

On the other hand, comparing the results in table 2 with table 4, table 5 with table 6, and table 8 with table 9 there is evident a significant effect of the upper-central region of the eye in determining orientation with respect to shade of background.

Another interesting fact that is evident from the data, is that when the remainder of the eye is stimulated by white or relatively strong light, the upper and lower halves of each retina are equally effective in determining the orientation of the crayfish. This is readily seen by comparison of the results of tables 4 and 9.

However, when one eye is stimulated by black in its lower half and the upper half of the other eye stimulated simultaneously by black, the animal orients itself, not at random due to opposing and equal stimuli as might at first be expected, but rather in the direction of the black stimulated lower half (compare table 10 with table 4). There is no significant effect of the asymmetrical stimulation of the upper halves of the two eyes. The animal is responding just as if only the lower half of one eye were stimulated by black. Thus, during simultaneous stimulation of the lower half of one eye and the upper half of the opposite eye with black, the lower half completely dominates the response.

Further evidence of a physiological dominance of the lower half over the

upper is seen in comparing the results obtained in table 5 with those in table 9. Here when the lower halves of the eyes are stimulated symmetrically by a black background the efficiency of the upper half in determining orientation is very much less than when the lower halves are symmetrically stimulated by light from a white background.

More, but less conspicuous, indications of the same type of relative dominance is seen in the results of tables 3, 6, and 7, where it is observable that when approximately the lower three quarters of the eyes are stimulated symmetrically or asymmetrically by black background reflected light, the effect of the upper quarter is less effective than when the lower three quarters are symmetrically stimulated by white (table 8).

These facts seem to demonstrate that the phenomenon of background selection in crayfishes is by no means one explainable in terms of simple phototropism. The fact of an asymmetrical stimulation of the two eyes by different shades of backgrounds is not sufficient to explain wholly the phenomenon. The crayfish central nervous system in conjunction with the compound eyes is adjusted physiologically to a background response. Mast ('23) has found similarly that the photic response of the fly *Eristalis* is determined by the portions of the retina stimulated. There is in crayfishes a dorso-ventral differentiation of the retina in the response mechanism with the central area in the dorso-ventral axis being the most effective. Furthermore, the eye is so adjusted in the system that, other things being equal, the crayfish turns in the direction of the darker underground. This seems to be a definite response to background and can perhaps be looked upon as an adaptive response.

SUMMARY

1. Nearly the maximum selection of one background over another is obtained when all the ommatidia which perceive light from images below the surface film (including that stimulation obtained from internal reflection) are stimulated by a black background in the one eye and by a white background in the other.

2. Under the above conditions black-adapted *Cambarus immunis*, when given a choice of black or white background, choose black about 85 per cent of the trials while white-adapted animals choose black about 79 per cent of the trials.

3. Those ommatidia directed upwards at angles greater than enough to perceive light from beyond the surface film (41° above the horizontal) are hardly sufficient to enable the crayfish to significantly select one background over another, though one eye has this portion stimulated by black and the other by white.

4. A decrease in the area differentially stimulated in the two eyes decreases the efficiency of the response, those ommatidia directed below the horizontal permitting a maximum of only about 71 per cent black selection.

5. When the other parts of the eyes are white or light stimulated, those ommatidia directed above the horizontal are as effective in determining orientation as those directed below the horizontal.

6. In the instance of simultaneous stimulation of the upper half of one eye and the lower half of the other with a black background, while the remaining portions of the eyes are stimulated by white or light, the lower half totally dominates the effect of the upper half.

7. When the lower halves of the two eyes are symmetrically stimulated by light from a black background, the effectiveness of the upper halves in determining orientation is diminished by the dominance of the former.

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FORESTS OF THE YARMOUTH AND SANGAMON INTER- GLACIAL PERIODS IN ILLINOIS¹

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The Pleistocene or glacial period, which lasted approximately one million years, brought about many changes in the stratigraphical, topographical and biotic conditions in the northern half of North America. During a portion of that period at least 4,000,000 square miles of land were covered with ice of enormous thickness. The Pleistocene may be divided into the following glacial and interglacial stages:

Nebraskan glacial stage
Aftonian interglacial stage
Kansan glacial stage
Yarmouth interglacial stage
Illinoian glacial stage
Sangamon interglacial stage
Wisconsin glacial stage
Recent interglacial stage.

The movement of the ice during each glacial stage was slow and its southern limit varied considerably for each stage. During the advance of the ice, the biota was greatly affected, it having been entirely obliterated or forced to migrate to other localities where conditions were more favorable for its existence. Whether or not there occurred during the past interglacial stages a succession of forests as extensive (Fuller, '35, Voss, '34, '37) as during the Recent stage cannot at present be affirmed or denied.

During the past fifty years numerous reports have appeared concerning the finding of remnants of interglacial vegetation many of which were encountered in well drillings, coal mine shafts, road and stream cuts. In many cases the identification of the materials was not carried out scientifically. Wood, for example, was sometimes identified by the odor obtained from burning it whereas in other cases the identification was based entirely on the external appearance of the wood sample.

With the recent developments in the field of plant histology and the introduction of the pollen analysis method, greater accuracy can now be obtained in the identification of the mega and microfossils. In the present study a method devised by Erdtman ('36) was used in isolating and concentrating

¹ This investigation was financed, in part, by a grant from the American Association for the Advancement of Science made through the Illinois State Academy of Science.

the pollen grains for analysis. This method is far superior to the one involving the use of potassium hydroxide. In brief the procedure is as follows: Peat, which has previously been dried over concentrated sulphuric acid, is pulverized and a quantity less than one gram is placed in a centrifuge tube. Four cc. of glacial acetic acid and 1 cc. of concentrated hydrochloric acid are added followed by 3 or 4 drops of sodium chlorate solution (sodium chlorate 1 part, water 2 parts). In a few seconds the peat becomes bleached due to the presence of chlorine. The material is then centrifuged, the fluid decanted, the sediment washed first with water and then with glacial acetic acid. The next step consists in acetolyzing the peat in order to remove the lignin and other polysaccharides. Nine cc. of acetic anhydride and 1 cc. of concentrated sulphuric acid are added and the centrifuge tube placed in a water bath which is heated to the boiling point. As soon as the water boils, the material is centrifuged, the liquid decanted, the sediment washed in water, then with dilute glycerin, and finally imbedded in glycerin jelly.

Accessible deposits of interglacial materials in Illinois are generally rare and even if they belong to the same interglacial stage, they may yet vary considerably in age. This is notably true of the Sangamon stage, one exposure may represent the early stage, the late stage or the entire period of deglaciation.

Subsequent to the recession of the ice of the second or Kansan glacial period, several changes, weathering and topographical, took place in the superficial layers of the newly exposed drift. Fresh glacial till after exposure to the atmosphere became oxidized and hydrated (Leighton and MacClintock, '30). This was followed by a leaching process in which calcium and calcium magnesium carbonates were removed by percolating ground water. A third and less rapid change was the disassociation or decomposition of the silicates and the solution of the cherts and quartzites.

DEPOSITS OF YARMOUTH INTERGLACIAL STAGE

Due to the filling of the pre-Kansan stream valleys with till and outwash materials, new drainage lines had to be formed (Leighton, '36). Conditions along interglacial streams were not unlike those found at present in stream valleys which have broad flood plains. With or without the formation of natural levees the margins of wide flood plains were often marshy permitting the growth of plants whose remains gave rise to peat deposits. The deposits were generally shallow and the purity of the peat depended upon the frequency of overflow. A peat of that type can now be seen in the valley of Mill Creek a few miles southeast of Quincy, Illinois, in Sections 21 and 22, T. 2 S., R. 8 W., Adams County (figs. 1, 2). In the Quincy deposit the layers which had the highest pollen frequency and the least amount of silt were found nearest the bottom. The abundance of *Larix* limbs some of which were four inches in diameter and the immense number of well-preserved

Larix and *Picea* leaves in the sections between the 16 and 26 inch, and between the 32 and 42 inch levels, suggested that the bottom land at one time was heavily wooded. The pollen diagram shows considerable variation in the percentages of the various species at different levels, however, the forest throughout the entire period of peat formation was essentially a northern conifer forest (fig. 3). Since the pollen frequencies between the 14 inch level and the top were so low, the percentages of the various types cannot be regarded as significant in that stratum.

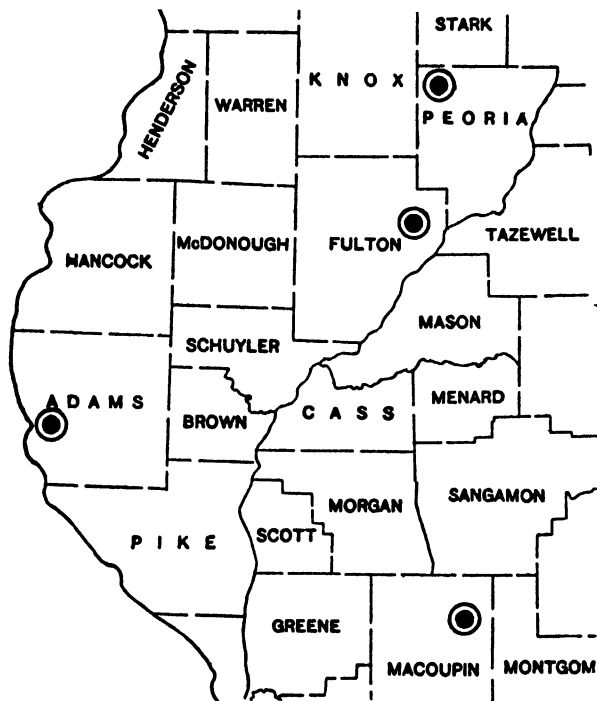


FIG. 1. Map of a portion of Illinois showing the location of the interglacial peat deposits.

Upon the organic layer rested a layer of alluvium six feet in thickness which lacked pollen and the superficial layers were weathered. The weathered surface is indicative of the interval of time during which the alluvium was exposed to the atmosphere preceding the advance of the Illinoian ice. The entire Yarmouth interglacial period as shown by its well developed soil profiles was at least two or three hundred thousand years in duration in contrast with the next younger interglacial interval, the Sangamon, which lasted approximately one hundred fifty thousand years (Leighton, '36). The forest history as revealed by the peat deposit represents only a portion of the entire Yarmouth period.

During the third or Illinoian glacial period the ice which had its center

of accumulation in Labrador reached its western limit a few miles east of Quincy. Above the Yarmouth alluvium are three feet of coarse gravel and nine feet of sand the upper layers of which are weathered, the weathering having taken place during the Sangamon interglacial interval. The above

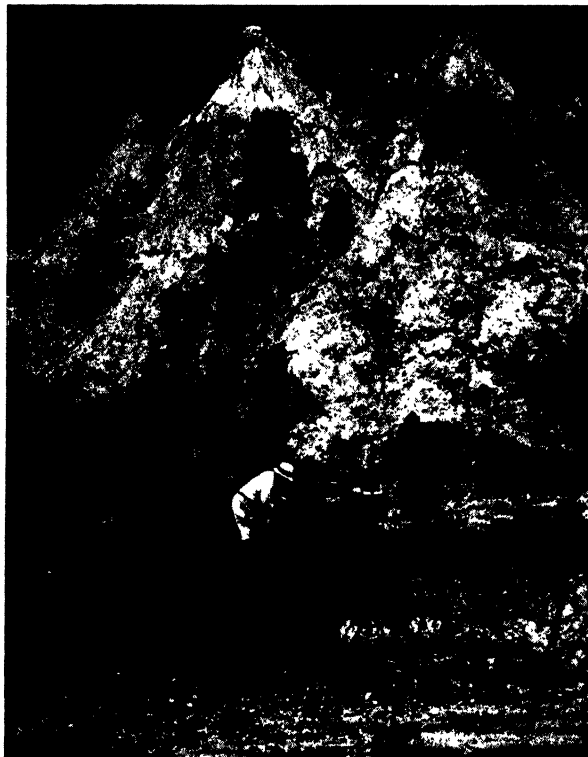


FIG. 2. Photograph of the Quincy exposure showing: (1) Peorian loess; (2) Sangamon loess; (3) Outwash gravel and sand; and (4) Yarmouth peat exposure.

mentioned layers of gravel and sand were deposited by waters flowing from the melting Illinoian ice. Superimposed in the outwash materials are twenty feet of loess, the lower layers of which were probably laid down during late Sangamon times when dust storms were frequent. The remaining loess known as Peorian owes its origin to the rock flour which was carried by the Mississippi from the melting ice of the Iowan lobe of the Wisconsin period. The rock flour was deposited on the river's banks, dried and carried eastward by winds, reaching its maximum thickness nearest the river (fig. 2).

Two and one half miles northwest of Nilwood, Illinois, in the southeast quarter of Section 10, Township 11N, Range 7W, Macoupin County, a layer of peat is exposed at the foot of a high bank on the northeast side of a tributary of the East Fork of Otter Creek. The peat, according to Dr. John R.

Ball of Northwestern University and the Illinois State Geological Survey who made a thorough study of the section, rests upon dark calcareous silt which in turn is underlain with sandy non-calcareous silt. Dr. Ball (personal com-

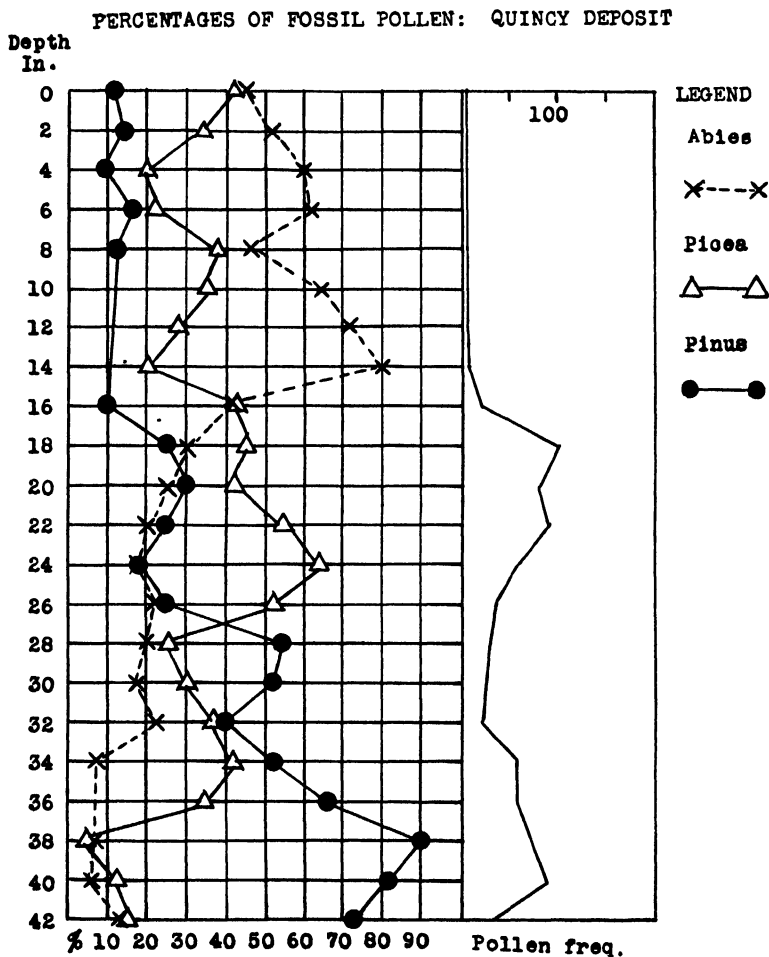


FIG. 3. Pollen diagram from the Quincy deposit.

munication) suggests that the non-calcareous silt may be indicative of a period of weathering prior to the oncoming of the Illinoian ice sheet. Directly above the peat is a very thin layer of fossiliferous clay and seventeen feet of Illinoian till. Above the till are five feet of loess.

Resting on weathered silt and covered with Illinoian till, the peat may be classified as late Yarmouth. The type of forest as revealed by the pollen analysis of the Nilwood deposit (fig. 4) was the same as the Quincy and the conditions under which the forest developed were doubtless the same. Dr. Ball

('37) and others have shown that the Yarmouth preglacial streams in the Nilwood region had wide floodplains, the swampy undrained areas of which were responsible for the development of the peat. The occurrence of certain

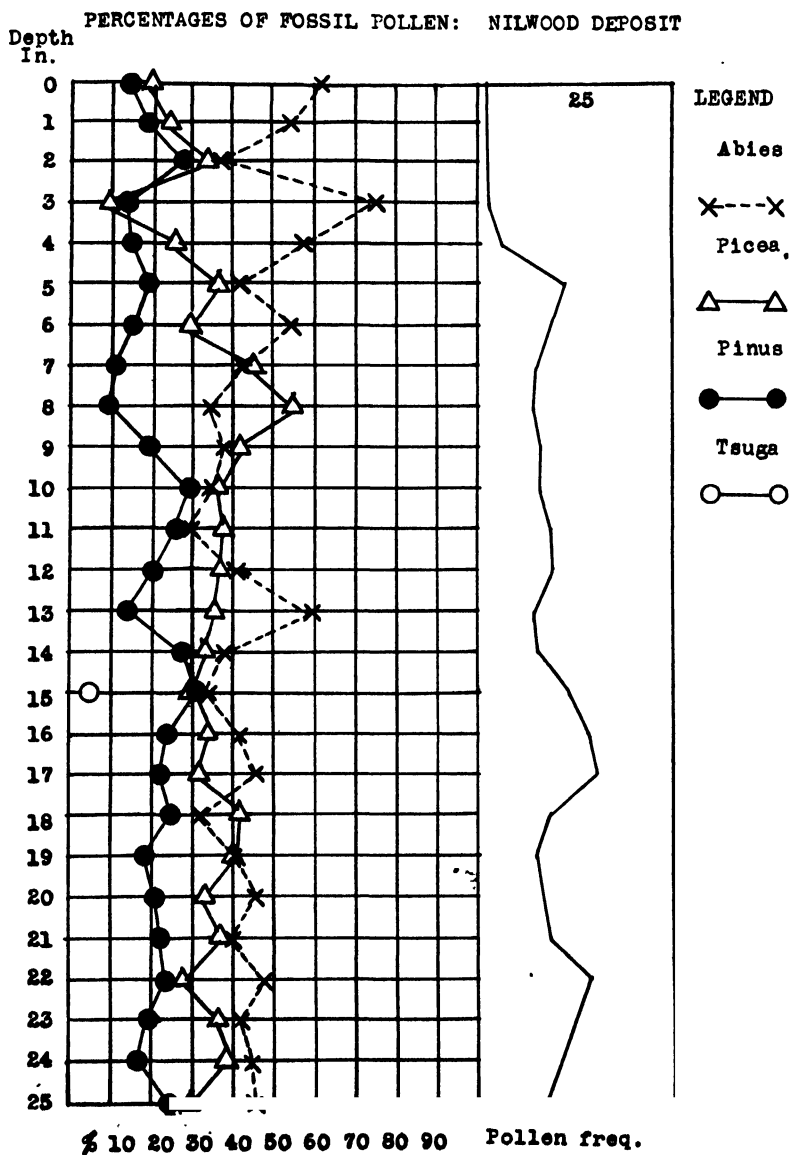


FIG. 4. Pollen diagram from the Nilwood deposit.

types of mollusca above the peat (Ball, '37) is also indicative of wide floodplains. In contrast with the Quincy peat, the pollen frequency was lower and its macroscopic material was smaller. The macroscopic remains were most

abundant in the upper layers and consisted entirely of leaves of *Abies* and branches and leaves of *Larix* and *Picea*, the largest piece recorded being a *Larix* branch one inch in diameter.

DEPOSITS OF SANGAMON INTERGLACIAL STAGE

A remarkable layer of Sangamon peat was recently exposed on the north face of the strip mine pit one and one-half miles south of Canton, Illinois, in Section 10, Township 6N, Range 4 E, Fulton County (fig. 5). The layer

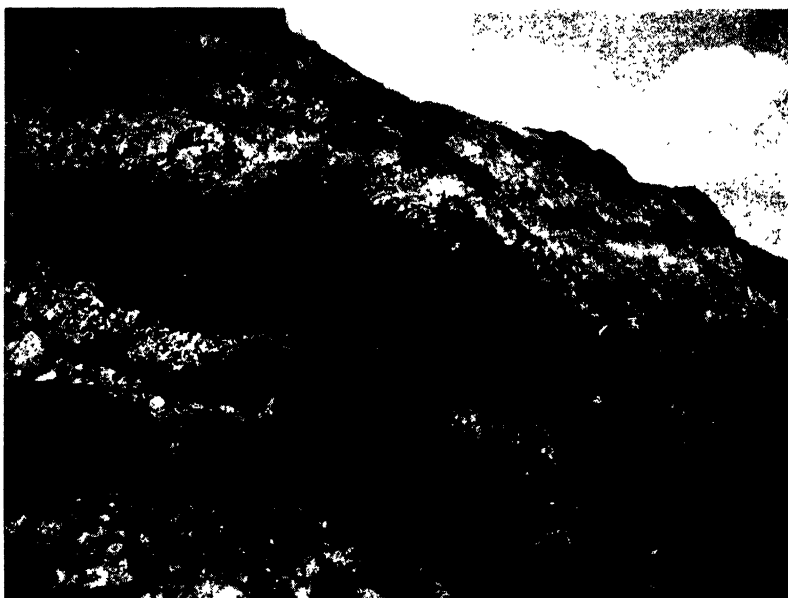
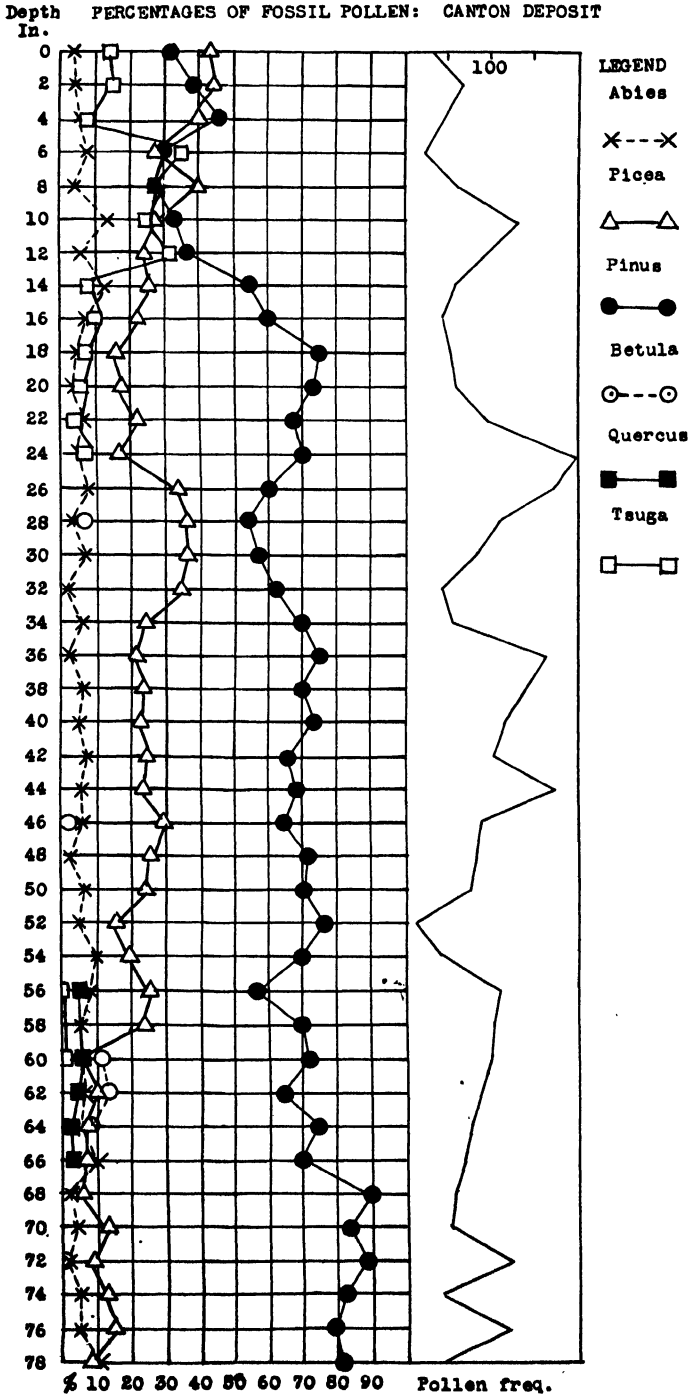


FIG. 5. Photograph of the Canton exposure. The material below the level of the pick handle is Illinoian gumbotil. Six and one-half feet of Sangamon peat rests on the gumbotil and fifteen feet of Peorian loess lies above the peat.

reached a maximum thickness of six and one-half feet at the eastern end of the pit and gradually became thinner as it extended westward for over a quarter mile. The peat lay on Illinoian till which presented a weathered surface in the form of gumbotil. It is highly improbable that the gumbotil developed while the peat was accumulating since downward circulation of water is necessary for the production of that type of soil profile (Leightor and MacClintock, '30, Weller, '30). Therefore a period which may be termed early Sangamon intervened between the end of till deposition and the beginning of peat accumulation. What the status of the plant cover was during early Sangamon times in central Illinois cannot at present be determined. The upper surface of the peat unlike that of the lower was undulating and



contained throughout practically the entire length of the exposure flattened roots, branches and trunks of tamarack trees. When edaphic conditions of the bog warranted the support of a coniferous forest the rate of peat accumulation equalled or became less than the disintegration of the surface materials and the thickness of the bog remained stationary. The contact between the peat and the overlying Peorian loess was not abrupt but instead consisted of thin alternating layers of organic soil and loess.

An examination of the pollen diagram shows that the conifers, *Abies*, *Picea*, *Pinus* and *Tsuga* were the predominant trees throughout the entire period represented by the peat deposit, *Pinus* being the most abundant (fig. 6). Between the 56 and 66 inch levels *Quercus*, although not having a high percentage, made its appearance together with *Betula* and *Tsuga*. The occurrence of *Quercus* pollen suggests one of two possibilities, either a migration and invasion of the conifer forest by the oak or the transportation by wind of oak pollen from a distant source. The Sangamon period in comparison with the Recent was of long duration and if data were available as to the southern extent of the conifer belt, one would be in a better position to state whether or not a slight extension of the deciduous forest northward took place similar to that which occurred during early Recent times.

Tsuga does not appear again above the 56 inch level until the 24 inch mark is reached. It gradually increases and reaches a maximum of 35 per cent at the 6 inch level and then declines to 13 per cent at the upper surface of the bog. With the exception of the small quantity of *Tsuga* pollen appearing near the bottom of the deposit, *Tsuga* appears in greatest abundance late in the history of the bog. In that respect the change in forest composition resembles that obtained by the writer from pollen studies of Recent bogs of the New England states.

The Laura deposit was uncovered during the construction of the hard road No. 78 underneath the Atchison, Topeka and Santa Fe Railroad tracks at Laura, Peoria County, Illinois. The peat was extremely wet due to the impervious quality of the underlying soil. On the whole the layer was very woody and can be classed as typical grass-herb-forest peat which is usually referred to by well drillers as the "chip pile" or if it contaminates the water of wells it is sometimes termed "Noah's cattle-yards."

The peat is of Sangamon age but whether or not it is early, middle, or late Sangamon cannot be determined until more topographical work is done and additional test drillings are made in that locality. Due to the proximity of the Illinoian Buffalo Hart moraine which lies a few miles west, the non-calcareous soil underlying the peat may be Illinoian outwash. If that is true then the peaty layer may be classified as Early Sangamon. On the other hand the underlying soil may be Sangamon alluvium and in that case the peat would have accumulated during the middle and late Sangamon periods.

There are several possibilities as to the age of the twelve foot layer of

loess or loess-silt which is superimposed upon the organic layer. The entire layer may all be Peorian loess or the upper portion may be Peorian loess with late Sangamon loess underneath. A third possibility involves the Shelbyville

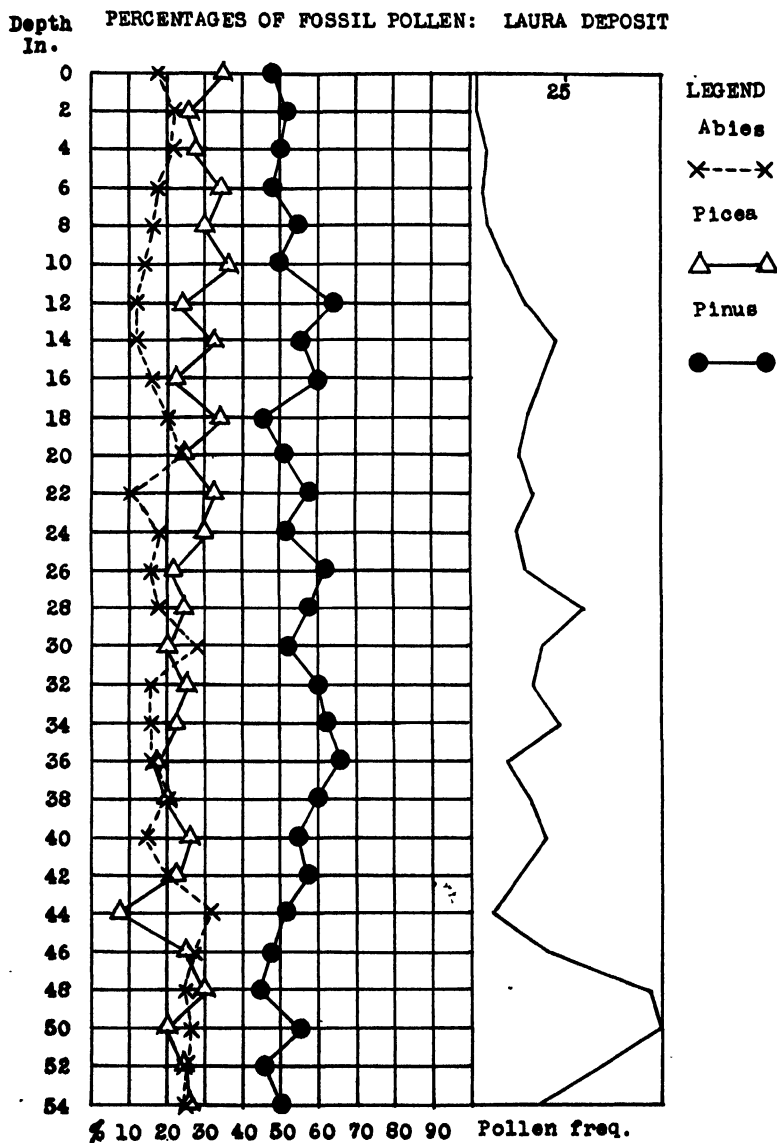


FIG. 7. Pollen diagram from the Laura deposit.

moraine which lies just five miles east of Laura. Beginning at the top the stratigraphical order might be as follows: post-Shelbyville loess lying on Shelbyville outwash and the outwash resting on late Sangamon loess.

The pollen diagram of the Laura peat is in many respects similar to that of the Canton, *Pinus* being the most abundant pollen with *Picea* and *Abies* represented in lesser numbers (fig. 7). In contrast the Laura deposit shows an absence of *Betula*, *Quercus*, and *Tsuga*. This absence may be due to several factors. The peat although of Sangamon age may be early, middle or late Sangamon and therefore the section may not be synchronous with that at Canton. On the other hand if it is practically the same age as the Canton formation, the lack of the types in question may be due either to the absence of those trees in the immediate vicinity at the time of deposition or the failure of the peat to preserve the pollen. The fact that the Laura peat contained much wood and also had a much lower pollen frequency suggests that the *Betula*, *Quercus*, and *Tsuga* which if present, may have disintegrated. No data dealing with differential pollen preservation in various types of peat are at present available.

SUMMARY

The pollen analyses of the Quincy and Nilwood peat which represent only a portion of the Yarmouth period reveal trees which can be regarded as climatic indicators and which suggest a cooler climate than the present. In general, that is also the conclusion drawn by Baker ('31) from his study of the terrestrial mollusca of Illinois associated with the Yarmouth interval.

With the exception of the interval in late Sangamon times when some deciduous trees were present, the late Sangamon together with early Peorian interval (Voss, '33) were characterized by the dominance of northern conifer forms.

The writer is indebted to Dr. George D. Fuller of the University of Chicago for suggestions and to Dr. George E. Ekblaw of the Illinois State Geological Survey and to Dr. John R. Ball of Northwestern University and the Illinois State Geological Survey for geological data.

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VARIATION IN THE TRANSPARENCY OF THREE AREAS OF THE ATLANTIC THROUGHOUT THE YEAR

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Our previous measurements of the penetration of daylight into the western North Atlantic Ocean have revealed striking differences in the transparency of the water and hence in the intensity of the illumination to which aquatic animals and plants are subjected (Clarke, '36, '39). However, these observations of light penetration have been confined to the summer months except for a series of observations made throughout the year at the western entrance of Vineyard Sound off Woods Hole (Clarke, '38). In the latter investigation a seasonal fluctuation in transparency of considerable magnitude was found and calculations showed that these variations must result in such large differences in the intensity of the light which reached organisms on the bottom or at mid-depths as to be of great ecological significance. In the study of the biology of the other oceanic areas, it was therefore important not only to compare the transparencies of the several regions at other seasons, but also to ascertain the magnitude of the changes in illumination which would be experienced during the year at one point.²

To this end measurements of light penetration were undertaken from the research vessel "Atlantis" on her nine cruises between Montauk Point, Long Island, N. Y., and Bermuda, from October 1937 to November 1938. On these cruises three areas of the ocean were traversed each characterized by a distinct type of water, and a standard station was established in each (Fig. 1): Station A in the *coastal water* which overlies the continental shelf; Station B in the "*slope*" *water* which extends between the continental slope and the Gulf Stream; and Station C in the *Sargasso water* which fills the whole of the central North Atlantic and of which the Gulf Stream is the western and northern edge. The three areas are of interest biologically because of the extreme contrast which they present. The plankton in the coastal water is abundant but composed of relatively few species. The Sargasso Sea is extremely barren in respect to plankton, although the number of species represented is large. The slope water is a zone of mixing between the other two areas. Bottom

¹ Contribution No. 236.

² The significance which variations in transparency would have for the photic reactions of animals living at great depths has been discussed elsewhere (Waterman, Nunne-macher, Chace and Clarke, '39).

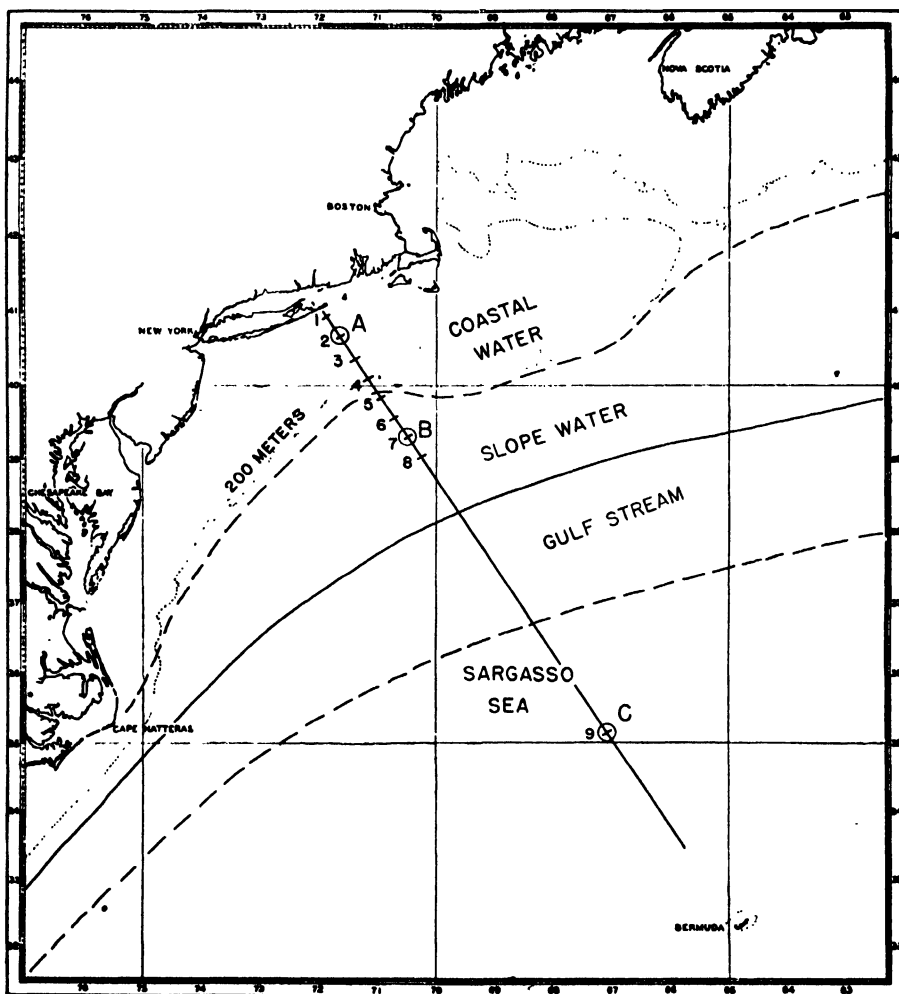


FIG. 1. Chart showing the areas in the Atlantic in which observations were made. The sharply delineated boundary of the Gulf Stream toward the coast is represented by a solid line; the more indefinite boundary toward Bermuda is indicated by a broken line.

fauna is much richer on the continental shelf than in deep water. Successful commercial fishing is limited almost entirely to the coastal region.

APPARATUS AND PROCEDURE

The measurements were made with two emission photocells of the Photronic type manufactured by the Weston Electrical Instrument Corporation: One of these was hung in gimbals and exposed on deck to the sun and sky; the other was placed in a watertight case provided with a plate glass window 10 cm. in diameter and lowered into the sea. The current generated by the

cell was measured by a Westinghouse Microammeter with full scale deflection of 25 μ a and a shunt for larger currents. Diffusing discs of flashed opal glass were used over the receiving windows of both the deck cell and the sea cell for all measurements. When used in full sunlight, the effective area of the window was reduced by placing a diaphragm with hole about 1.7 cm. in diameter over the diffusing disc. The intensities to which the cells were exposed were thus limited and the curvature of the response of our instruments within this restricted range was determined by comparison with a caesium photo-electric cell whose response was known to be linear (Powell & Clarke, '36).

The spectral sensitivity of the Photronic cell exhibits a maximum at 5800 Å and drops off to 10 per cent of the maximum at 7080 Å and at 3420 Å. Thus without a color filter the photometer was sensitivity to the total visible spectrum. At each station the photometers were used without filters for one series of measurements, and in as many cases as possible, a second series was undertaken in which the light reaching the instrument was confined chiefly within the green region of the spectrum. This was accomplished by placing beneath the diffusing discs of both photometers a Schott-Jena filter of type VG-2³ (practically identical to type VG-9). The transmission of this filter reaches a maximum at 5300 Å and drops off to 10 per cent of the maximum at about 6200 Å and 4600 Å. The point of maximum sensitivity of the combination of cell plus filter can safely be taken as about 5500 Å and thus corresponds closely to the spectral sensitivity of the human eye.

The measurements at sea were carried out by Mr. Dean F. Bumpus, Biological Technician for the Woods Hole Oceanographic Institution. The ship was first hove to with her stern directed toward the sun, and the submarine photometer was suspended from the end of the mizzen boom. The shadow of the ship's hull was thus avoided.

Changes in the temperature of the Photronic cells, which had been found to affect the emission of the instruments (Waterman, Nunnemacher, Chace and Clarke, '39), were reduced to a minimum by lowering the submarine photometer into the water and placing the deck photometer in position long enough before measurements were begun for them to come into thermal equilibrium with the water and air respectively.

The submarine photometer was raised to a point just about the surface for the first measurement and its emission compared with that of the deck photometer. The observed ratio was taken as 100 per cent. The submarine photometer was then lowered successively to depths of 2,⁴ 6, 10 m., every

³ In four of the earliest measurements Schott-Jena filters BG-18 and GG-11 were used together instead of VG-2. This combination allows essentially the same transmission. Series 467, which was made with BG-18 and GG-11 and series 468, made with VG-2 and carried out immediately afterwards at Station B yielded almost identical curves for light penetration.

⁴ When possible a measurement was made also at 1 m., but the action of the waves

TABLE I. Summary of measurements of light penetration and comparison of extinction coefficients for the total visible light and for the green component of daylight

Date	Atlantis Station	Weather	Sea	Wind	No Filter					Green Filter				
					Series	Range in m.	k, Average extinction coefficient	Per cent average absorption per meter	Per cent surface light at 2 m.	Series	Range in m.	k, Average extinction coefficient	Per cent average absorption per meter	Per cent surface light at 2 m.
Station A—Coastal Water														
Oct. 2, '37	2904	BC-C	3	3	452	1-48	.14	13	45	453*	1-38	.12	11	60
May 17, '38	3038	B	2	3	464	1-54	.11	10	59					
May 18, '38	3041	O	2	3	465	2-54	.12	11	66	465A*	2-20	.11	10	70
July 17, '38	3111	O Fog	1	1	477	2-60	.14	13	65	478	2-44	.13	12	74
Sept. 3, '38	3153	BC	1	1	485	2-60	.11	10	70	486	2-50	.11	10	80
Sept. 29, '38	3157	C Fog	1	2	487	1-40	.15	14	66	488	1-25	.17	16	69
Nov. 3, '38	3215	BC	1	1	487	1-40	.15	14	66	494†	1-25	.16	15	—
Station B—Slope Water														
Oct. 5, '37	2912	BC-C	3	3	454	1-76	.065	6.5	70					
Jan. 4, '38	2943	BC	2	1	457	1-107	.050	5.0	79					
Apr. 12, '38	3031	B	3	3	462	2-49	.10	10	63	463*	2-20	.11	10	70
June 1, '38	3052†	B	1	1	466	1-110	.065	6.5	64	467*	2-70	.079	7.9	71
June 1, '38	3052†	B	1	1	466	1-110	.065	6.5	64	468	2-65	.077	7.7	65
July 14, '38	3105	B	5	5	475	4-121	.058	5.8	—	476	4-74	.062	6.2	—
Sept. 1, '38	3149	C	2	2	484	2-101	.066	6.6	82	483	2-59	.071	7.1	75
Nov. 2, '38	3212	B	2	2	493†	2-70	.096	9.6	73	492†	2-50	.087	8.7	75
Station C—Sargasso Water														
Oct. 9, '37	2924	C	3-4	2-3	455	2-129	.042	4.2	63					
Dec. 10, '37	2931	C	1	1	456	2-120	.047	4.7	78					
Jan. 7, '38	2945	BC	2	2	458	2-91	.059	5.9	74					
Apr. 7, '38	3025	R.Q.O.	1	1	461	2-59	.066	6.6	51?					
June 5, '38	3062	B	4	3	469	2-135	.051	5.1	68	470	2-90	.059	5.9	74
July 9, '38	3093	BC	1	1	471	5-131	.054	5.4	—					
July 10, '38	3093	BC	2	2	474	2-131	.053	5.3	70					
Aug. 29, '38	3147	C	2-3	2-3	481	2-113	.044	4.4	48?	473	2-94	.056	5.6	63
Oct. 7, '38	3174§	C	1	1	489	1-127	.047	4.7	73	482	2-78	.048	4.8	70
Oct. 27, '38	3200	BC	1	1	489	1-127	.047	4.7	73	491†	2-50	.066	6.6	82

* Measurement made with Schott-Jena filters BG-18 and GG-11. Filter VG-2 used for all others in this column.

† Measurement made with Westinghouse "Photox" cell.

§ Observation made 13 miles NW of Station C.

5 m. to 30 m., every 10 m. to 60 m. and every 15 m. to the greatest depth at which a reading could be obtained. The "corrected" vertical depth of each reading was obtained by multiplying the length of the supporting cable by the cosine of the angle which it made with the vertical as it entered the water. The value obtained at each depth was corrected for the curvature in the emission of the cell and calculated as a percentage of the light reaching the surface of the sea. Since both the submarine photometer and the deck photometer were read for each depth, every measurement is independent of the others and therefore the average transparency for the whole series at each station is a highly reliable value.

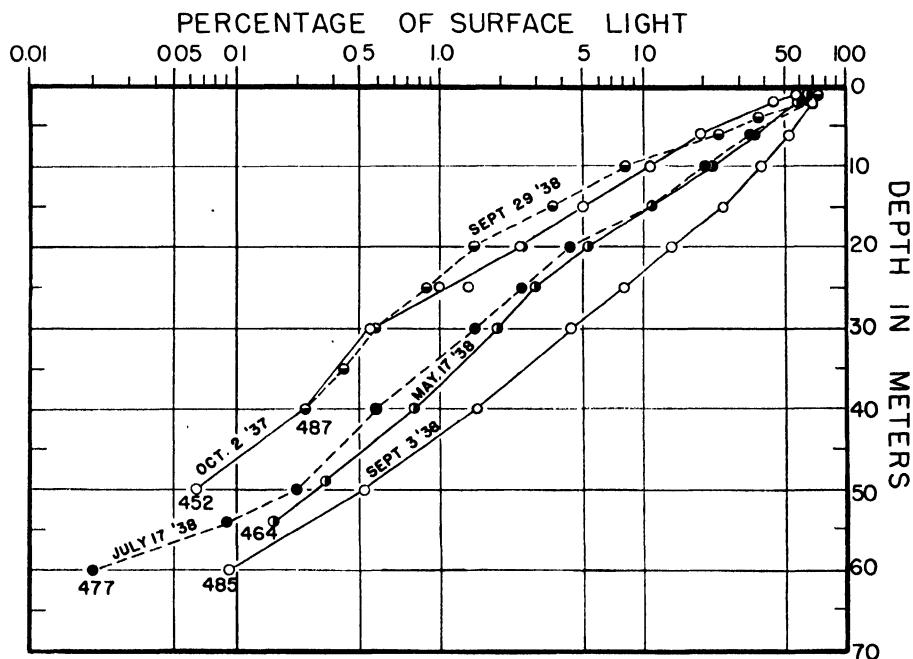


FIG. 2. Coastal Area—Station A. Relation between depth and total visible light (photometer without filter) expressed as a percentage of the light just over the surface (logarithmic scale). Series number indicated at the end of each curve (see Table I for data).

The apparatus and procedure conform to the recommendations of the Subcommittee on Light Measurements of the International Council for the Exploration of the Sea (Atkins, Clarke, Pettersson, Poole, Utterback and Angstrom, '38).

OBSERVATIONS

The observations of light penetration in the three areas under consideration are summarized in Table I and a large number of the individual series rendered readings near the surface highly inaccurate and occasionally reliable measurements could not be obtained short of 6 m.

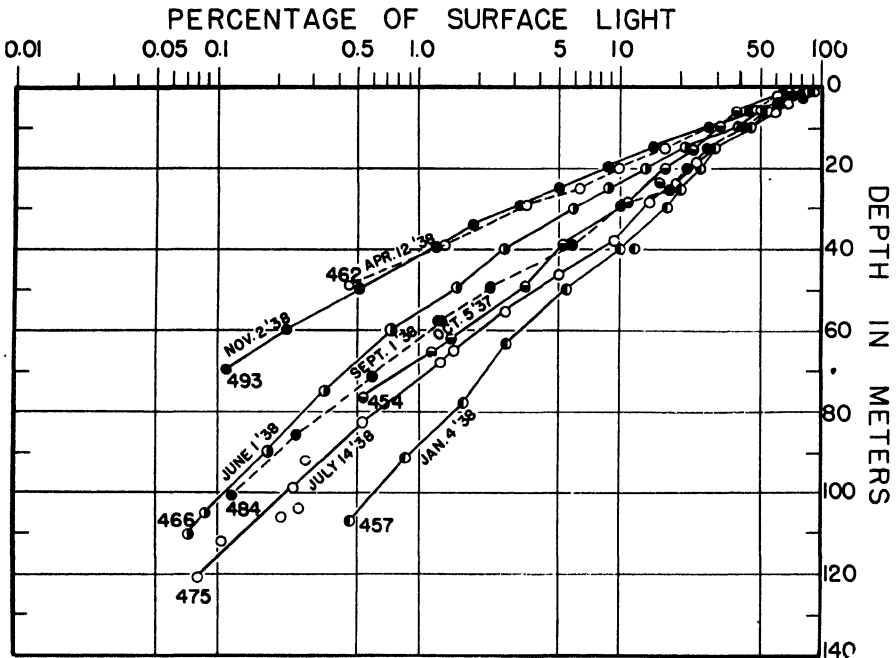


FIG. 3. Slope water—Station B. Relation between depth and total visible light (photometer without filter) expressed as a percentage of the light just over the surface (logarithmic scale). Series number indicated at the end of each curve (see Table I for data).

of measurements are presented graphically in figures 2, 3, and 4. It will be observed that in spite of variable sea and sky conditions readings which make up each series are consistent and for the most part fall on a remarkably straight line in a semi-logarithmic plot. The water is thus known in most cases to have been highly homogeneous optically over the range studied. Consequently it is legitimate in comparing one series of measurements with another to use the *average* value of the extinction coefficient⁵ or the average percentage absorption per meter.

The extinction coefficients for the measurements of the total visible spectrum made with no color filter over the photometers are seen from Table I to be closely followed for depths greater than 2 m. by the values for the green component of daylight only (see also Fig. 6). This parallelism may be explained by the rapid absorption of the light at the two ends of the spectrum by the first few meters of water with the result that in the deeper strata the light is largely confined to the central part of the spectrum. The remaining light

⁵ The extinction coefficient is defined as k in the equation $\frac{I}{I_0} = e^{-kL}$ where the intensity of the light is reduced from I_0 to I in the depth L expressed in meters. See Whitney ('39) for a more elaborate form of this equation.

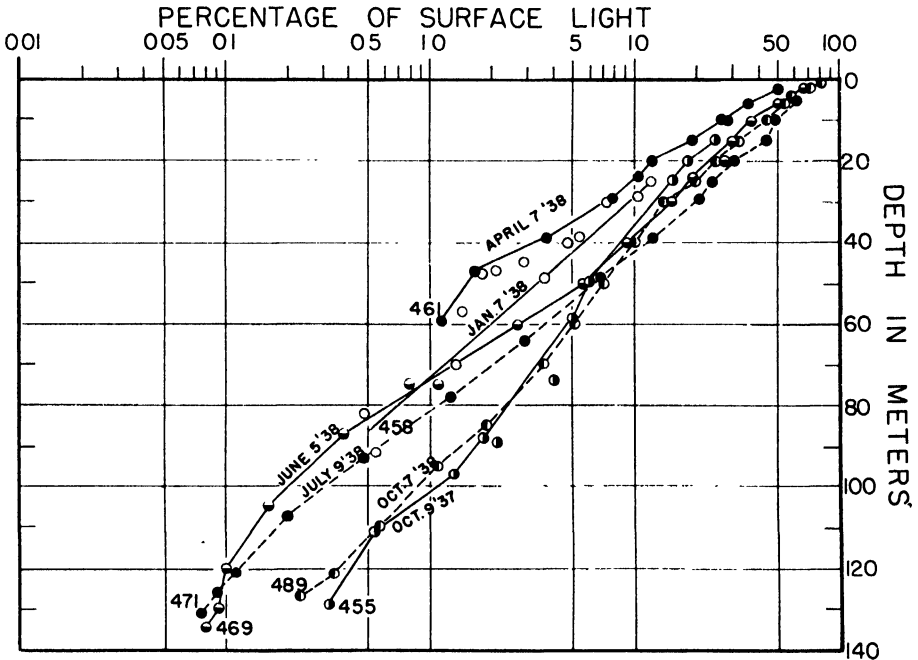


FIG. 4. Sargasso Sea—Station C. Relation between depth and total visible light (photometer without filter) expressed as a percentage of the light just over the surface (logarithmic scale). Series number indicated at the end of each curve (see Table I for data).

would therefore exert the same effect on the photometer whether used with or without the green filter. This explanation is borne out by a comparison of the percentage of the surface light which was observed to remain at a depth of 2 m. in the two cases (Table I). In practically every instance the photometer measuring the total light (no filter) indicated a greater reduction at 2 m. than was the case when the instrument was limited to the green component. For a detailed study of the seasonal and regional differences in general transparency below 2 m. either set of data may be used and the two sets serve as a check on each other. Actually the measurements with no filter will be considered below since we have more of these series.

Coastal Water—Station A

The measurements at Station A extended nearly to the bottom which varied in depth between 63 m. and 75 m. The water exhibited a rather uniform transparency at all depths on every occasion that the station was visited. Slight but definite changes in the slope of the curves occurred at 20 m. on September 29, 1938, and at 30 m. on October 2, 1937, and these differences in transparency were encountered at exactly the same depths in the succeeding

measurements with the green filter. The indicated changes in rate of light penetration are therefore real and not due to instrumental or observational errors. The water in this region becomes very highly stabilized during the summer and early autumn months because of thermal stratification. (For example, on July 17th the temperature changed abruptly from 20° C. at 10 m. to 7° C. at 35 m.) Under such circumstances the water is not easily mixed and material influencing absorption can accumulate locally (Pettersson, '34; Oster and Clarke, '35; and Whitney, '38). Although we have no information in the present case as to the precise agent responsible, a similar explanation undoubtedly accounts for the changes in transparency with depth.

Throughout the period of observation the average absorption per meter at this station varied from a maximum of 14 per cent (extinction coefficient, $k = .15$) on September 29, 1938, to a minimum of 10 per cent ($k = .11$) on September 3, 1938, and May 17, 1938. There appears to be no particular seasonal trend in the changes of transparency, but irregular fluctuation would be expected in the water at this station which is subject to so many disturbing influences. The strength of the wind, the stability of the water, and the abundance of plankton and its derivatives all vary widely. At times when stirring by wind, tides, or currents is effective, the nearness of the shore and of the bottom makes it possible for obscuring material to be introduced rapidly into the water. Consistent with this view is the fact that the seasonal variations in transparency at Station A are not as great as those observed by Clarke ('38) for a station off the western entrance to Vineyard Sound—a location also to be included in the "coastal area," but much closer to shore. The transparency of the water at Station A at all times corresponded to the lower absorption values observed off Vineyard Sound.

Slope Water—Station B

Since Station B was located some distance beyond the edge of the continental shelf the depth of the water was very much greater (about 2600 m.), and although the light penetration observations extended to a maximum of 121 m., the stratum measured represents only a small fraction of the total depth. The curves for the individual series (Fig. 3) are all relatively straight, indicating homogeneous water, although slight changes in slope are to be observed as for example in the measurement of October 5, 1937. The absorption of light at this station varied from a maximum of 10 per cent per meter ($k = .10$) on April 12, 1938, to a minimum of 5 per cent per meter ($k = .050$) on January 4, 1938.

This relatively great fluctuation in the clearness of the water would appear strange for a location in deep water well removed from the shore if it were not for the fact that the slope water has been shown to be a region of extensive mixing (Iselin, '36). Eddies of the clearer Sargasso water tend to be ejected from the western edge of the Gulf Stream and to mix with eddies

of the more turbid coastal water which have drifted out from the continental shelf. In the intervening region of slope water patches containing a high percentage of Sargasso water or of coastal water might thus be expected to occur before mixing became complete. This suggestion is well substantiated by figure 5 in which salinity is plotted against depth (for the upper 300 m.) for the

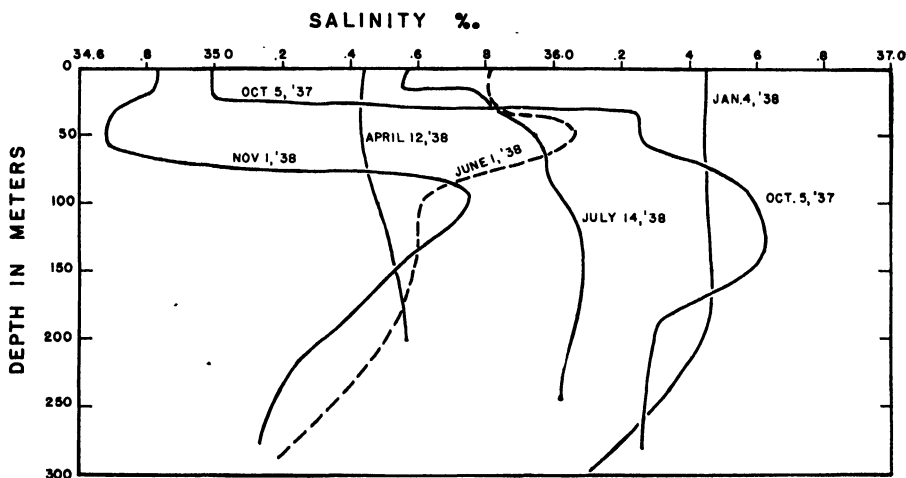


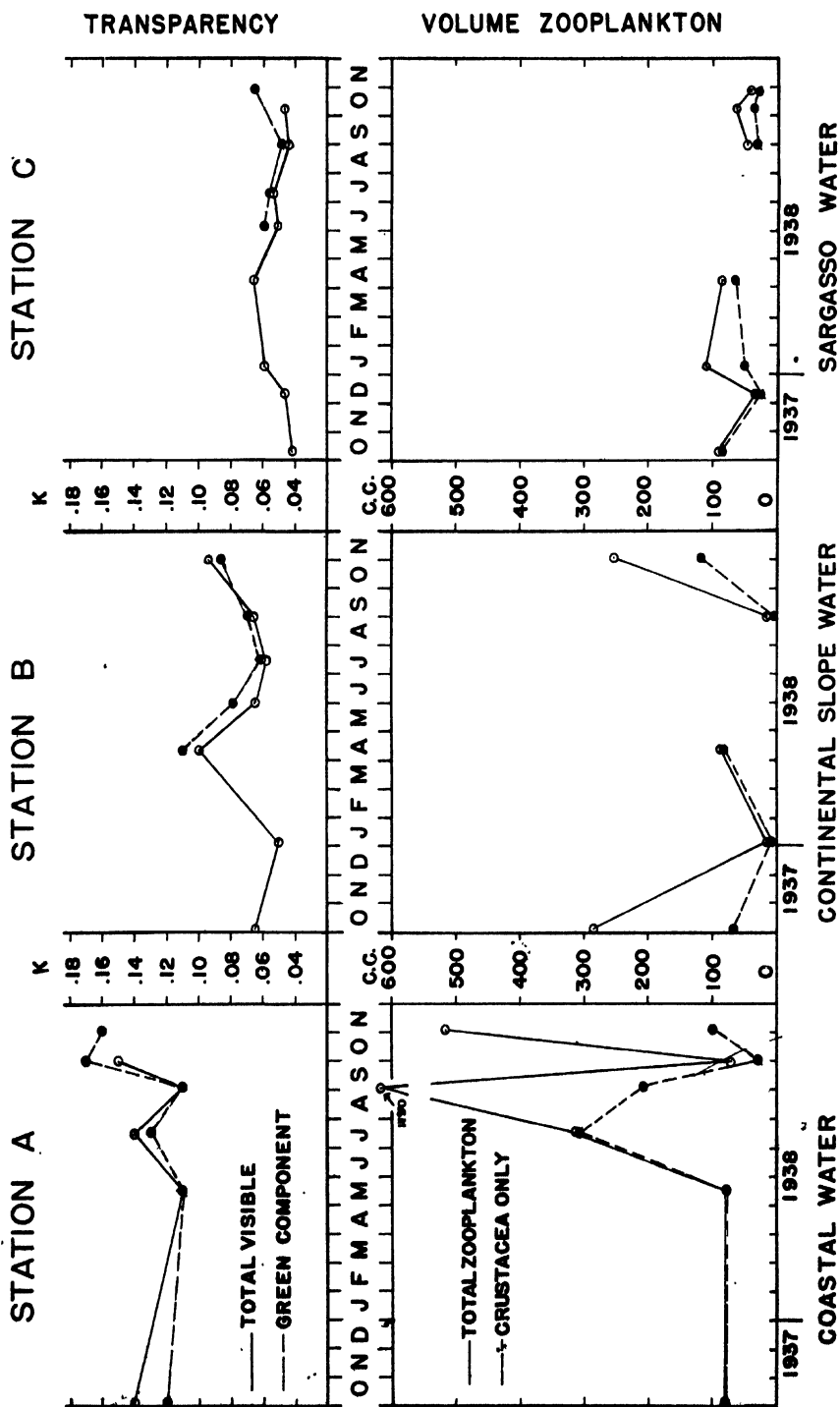
FIG. 5. Relation between depth and salinity in the slope water (Station B).

several occasions on which Station B was visited.⁶ On January 4, 1938, almost pure Sargasso water was present, as is shown by the occurrence of salinities higher than 36.0 per cent. The unusually high transparency on that date is thus directly explained. On the other hand, the low salinities which obtained on April 12, 1938, and, in the upper strata, on November 1, 1938, indicate a considerable admixture of coastal water and account for the less effective penetration of light. On October 5, 1937, an exceedingly abrupt change in salinity was encountered at about 20 m., and although the depth of the transition does not correspond exactly to the change in slope of the light intensity curve, one observes that the uppermost water layer was less transparent on this date than on any other occasion. Salinities and transparencies of intermediate values were encountered on the remaining visits to this station.

Sargasso Water—Station C

At Station C the water was sufficiently clear to allow measurements to be extended to a maximum depth of 135 m., but since the bottom here was at about 5200 m., the illuminated stratum was an even smaller fraction of the total depth than at Station B. Although the water appeared to be optically homogeneous because of the essential straightness of the curves (Fig. 4), the individual measurements were somewhat irregular due in part to adverse

⁶ I am indebted to Mr. C. O. Iselin for this information.



weather and in part to the greater error in estimating the exact vertical depth with longer lengths of wire out. The absorption of light varied from a maximum of 6.6 per cent per meter ($k = .066$) on April 7, 1938, to a minimum of 4.2 per cent per meter ($k = .042$) on October 9, 1937. The slight differences in transparency observed are probably not assignable to any one of the environmental factors, all of which are usually highly constant in this area. The salinity at every depth down to 300 m. was confined between values of 36.1 and 36.7 on all occasions. The temperature at the surface varied only between 20° and 27° C., and at 100 m. it ranged between 18° and 23° C. In neither case was correlation with transparency observed.

DISCUSSION

A comparison of the three areas throughout the year shows that in spite of the variations in transparency at each station, the absorption rates in the several regions overlap to only a slight extent (Fig. 6). The average values for each differ distinctly and allow the general conclusion to be reached that the Sargasso water is the most transparent, that the coastal water is much less clear, and that the slope water is intermediate (Table II).

TABLE II. *Comparison of average absorption and of absolute and relative variation in the three areas*

Area	Absorption per meter		
	Range	Average	Relative variation
	<i>Per cent</i>	<i>Per cent</i>	<i>Per cent</i>
Coastal water	10-14	12 ($k = .13$)	33
Slope water	5-10	7.1 ($k = .071$)	70
Sargasso water	4.2-6.6	5.1 ($k = .051$)	47

The slope water exhibits the greatest absolute variation and also the greatest variation relative to the value of the average absorption. The absolute variation in the coastal water is somewhat less and in the Sargasso water is very much smaller than in the slope water. The *relative* variation of the coastal water, however, turns out to be somewhat less than the *relative* variation of the Sargasso water because of the high values for the absorption of the coastal water. The fluctuations in the transparency of the Sargasso water, the absorption of which is nearly as low as that of distilled water (Clarke and James, '39), would be accounted for by extremely slight changes in the amount of absorbing material present. For the variations observed in the coastal water the addition or removal of much larger amounts of obscuring matter would be required.

These differences in the average values of transparency and in the amount

of variability have been shown above to correspond to important differences in the hydrography of the areas. But differences in the temperature and salinity of the water do not themselves influence transparency significantly; they merely indicate the derivation of the body of water in which the measurement was made. Thus we have seen that the water at Station C was at all times typical of the Sargasso Sea area, the water at Station A exhibited the variability characteristic of the coastal area, and the water at Station B was on some occasions similar to coastal water and on some occasions was nearly identical to Sargasso water. Our ultimate problem, therefore, is to determine the cause of the difference between the transparency of Sargasso water and of coastal water and to explain the greater variation in the amount of obscuring material in the latter.

The high transparency of the Sargasso Sea is due in part to the long interval since the water in that area has been in contact with the bottom or with the shore, and the consequent opportunity for mud particles to settle out, and in part to the paucity of the plankton (Fig. 6). In the coastal area detritus is introduced from the shore wherever wave action or tidal turbulence is strong or rivers debouch and from the bottom whenever vertical stirring is sufficiently effective to reach the bottom, as it is on the continental shelf during the winter months. In addition the plankton is abundant and extremely variable in the coastal water, as is apparent from figure 6 (see also Bigelow and Sears, '39).

A close scrutiny of figure 6 shows, however, that no exact correlation is indicated between the abundance of the total zooplankton, or of the crustacea, and the changes in transparency. No hauls were made at these stations specifically for the quantitative study of the phytoplankton, but diatom material was found in the zooplankton nets during periods of flowering. None of these occurrences corresponded to the high values for the extinction coefficient. On May 17, 1938, at Station A, the transparency ($k = .115$) was practically identical to the value observed on May 18, 1938 ($k = .116$), at a station only 10 miles distant, although in the first case the scrim net catch in the upper 25 m. (total volume 57 cc.) was composed entirely of crustacea and in the second case the corresponding catch (total volume 112 cc.) contained 109 cc. of ceratium and only 3 cc. of crustacea. We may conclude therefore that the changes in transparency at our three stations were not due *directly* to the abundance of either the zooplankton or the phytoplankton. A similar conclusion was reached by Poole and Atkins ('29) and by Clarke ('38), but Williams and Utterback ('35) found "considerable correlation" with the total plankton.

An *indirect* relationship may exist, however, between the abundance of plankton and transparency in that the animals and plants may affect the rate of light absorption after they have died and disintegrated. The decomposing plankton material may accumulate in clouds and exert an obscuring effect, it

may sink to the bottom and add to the detritus later to be stirred up, or it may influence light absorption after it has gone into solution. Probably the finest particles have the greatest effect on the transparency of the sea. Clarke and James ('39) found that the transmission of samples of sea water was greatly increased by filtering through a Berkefeld candle. Furthermore, even after Berkefeld filtering, samples of coastal water exhibited a highly selective action on light (beyond that of pure water itself). Thus coastal water was shown to contain material of filter-passing dimensions which exerted an important influence on transparency. Accordingly, an area of the ocean with an abundant and variable plankton would be expected to fluctuate in respect to transparency although no exact correlation be found with the catches of living plankton. Whether this indirect action of the plankton has a greater or a lesser effect on transparency than the periodic admixture of mud from the bottom and the shore remains to be determined. There is no doubt that the progressively reduced influence of both these factors in the slope water and the Sargasso water accounts for their greater clearness.

The effect which the foregoing variations in *rate* of absorption will have on the intensity of the submarine illumination is very different depending upon the depth of water considered as well as upon the magnitude of the extinction coefficient. An organism living at a depth of 50 m. in the slope water would have received a percentage of the surface light which was about $12 \times$ greater when the water was the clearest than when it was the most turbid (Table III).

TABLE III. *Effect of variation in transparency on the illumination at two depths in the three areas*

Area		Percentage of surface light reaching designated depths *		
		Maximum Per cent	Minimum Per cent	Average Per cent
Coastal water	50 m.	0.41	0.06	0.15
Slope water	50 m.	8.2	0.67	2.9
Sargasso water	50 m.	12.2	3.7	7.8
Slope water	500 m.	2×10^{-9}	2×10^{-20}	4×10^{-14}
Sargasso water	500 m.	8×10^{-8}	3×10^{-13}	8×10^{-10}

* Disregarding "surface loss."

In the coastal water, at the same depth, the difference produced by the variations observed in the transparency would make a 7-fold change in the illumination, whereas in the Sargasso Sea the light at 50 m. would be only a little more than $3 \times$ as bright on one occasion as on another.⁷ At a depth of 500 m., however, in the Sargasso Sea the proportion of daylight present would be more than $100,000 \times$ greater when absorption was at a minimum than when it was at a maximum (if we assume that the water below the greatest depth

⁷ Disregarding seasonal changes in the intensity of daylight, (Clarke, '38).

of actual measurement had the same transparency as that above). In the slope water a difference as great as $10^{11} \times$ would be encountered at 500 m. (see also Waterman, Nunnemacher, Chace, and Clarke, '39). It is therefore apparent that even slight differences in the transparency of oceanic waters produce great changes in the illumination beneath the surface and these must be of tremendous importance to photosensitive plants and animals.

SUMMARY

1. Measurements were made throughout the year 1937-38 of the penetration of daylight into the sea at single stations located in the coastal area, the slope water area, and the Sargasso Sea between Long Island, N. Y., and Bermuda using Weston photronic cells with and without green filters.

2. The water was found to be optically homogeneous over the range of depth investigated in almost all cases and no significant difference existed below 2 m. in the rates of absorption of the total visible spectrum and of the green component of daylight.

3. The coastal water was the least transparent on all occasions (average absorption 12 per cent per meter), the Sargasso water was the clearest (absorption 5.1 per cent) and the slope water was intermediate (absorption 7.1 per cent).

4. Variation in transparency was greatest in the slope water area and is accounted for by the fluctuations in the amounts of Sargasso water and coastal water present. The variations in the other areas are not correlated directly with the plankton but may be, indirectly, through its disintegration products.

5. Very large changes in the illumination reaching the deeper strata, which must be important biologically, are produced by even slight variations in transparency.

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A FLORISTIC STUDY OF A DEVELOPING PLANT COMMUNITY ON MINNESOTA POINT, MINNESOTA

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Minnesota Point, a sand bar about seven miles long south of Duluth, Minn., separates Lake Superior from Superior Bay which connects with St. Louis River Bay. It is opposed by Wisconsin Point three miles long, originally a part of the same sand bar through underwater connections. Between these two Points, is the Superior entrance channel, the natural outlet of St. Louis and Nemadji Rivers. The Duluth entrance channel is artificial. The highest elevation of the dunes and ridges is about twenty-four feet above the lake level. Its natural width has varied from less than two hundred to five hundred yards. At present it is considerably wider in places along Superior Bay shore due to sand-fills made by dredging the navigation channel. On one of these sand-fills the present study was made.

The sand-fill adjoining Oatka Beach Addition along Minnesota Avenue between 40th and 43rd streets, about 3.5 miles from the north end of the Point, was made during the summer of 1935 by the United States Engineering Department. It comprises an area of 29.7 acres. The sediment consists of sand and silt. The general elevation of the sand-fill is only a few inches above the bay level. On the bay side of the sand-fill in the fall of 1935, there were many shallow ponds and depressions which became modified during subsequent years by sinking of the soil, erosion by wave action and by the developing vegetation into a marsh, one to two feet deep. The northwest corner of the sand-fill became an island, cut off by a shallow channel diagonally through the marsh. During the summer of 1938 with unusually high water level, the west shore was eroded by wave action while deposition took place along the north and south shores. Thus, at present, it is somewhat narrower and longer than originally.

PIONEER VEGETATION

This new area lay open to plant invasion by winds and water. In the fall of 1935 when the author first saw it, the plant community was in its initial stages of development. So sparse was the population that the area at a distance appeared bare. However, a closer study revealed scattered individuals of annuals, biennials and perennials of which five species were in fruit. This pioneer plant community inspired the author to undertake the study of the developing vegetation as to its floristic composition.

The annual pioneers fruiting the first year, the fall of 1935, were *Bidens cernua*, *B. comosa* and *Polygonum persicaria*. They were widely scattered in shallow depressions of water among species of *Carex*, *Juncus*, *Scirpus* and various grasses in vegetative stages of growth. Of the perennials, *Carex scoparia* and *Juncus brevicaudatus* were in fruit. No attempt was made to determine the non-fruiting species except *Typha latifolia* and *Scirpus validus* which were in seedling stages. The only biennial noted was *Senecio palustris* in rosette stages. There were also rosettes of *Lepidium*. The woody perennials were represented by numerous seedlings of *Salix* two to three inches high.

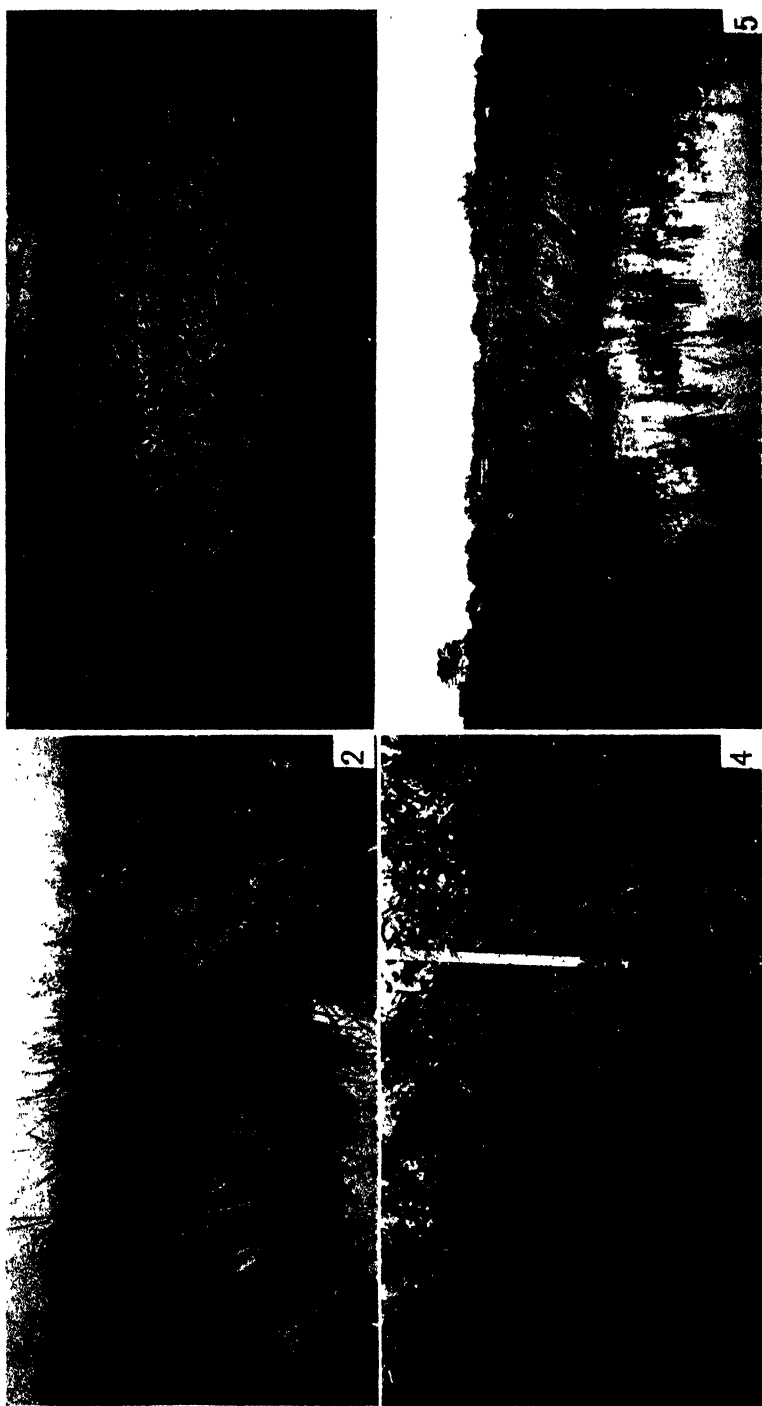
SECOND YEAR VEGETATION

During the spring 1936, the most rapidly growing species was *Senecio palustris* (L.) Hook. (fig. 1). The many, large and vigorous rosettes of the previous season sent forth hollow, leafy stems two to three feet high,



FIG. 1. *Senecio palustris*, a rapidly growing species, a dominant pioneer in 1936.

with diameter from one to two inches at the base. In vernal aspect the area appeared yellow due to the abundant flowers which later matured into fruit. In July and August the second germination was taking place; new rosettes appeared on shores still free from other vegetation.



FIGS. 2-5.

FIG. 2. A *Bidens-Typha* community during the summer of 1936.

FIG. 3. *Agrostis stolonifera* forming dense mats in shallow water.

FIG. 4. A dense willow thicket developed during the third year.

FIG. 5. The *Typha-Scirpus* marsh and the willow zone in 1938.

On May 29, a list quadrat, 10 m. square, was laid out about ten feet from the bay shore. The plant count revealed 262 willow seedlings about four inches high. In the southeast corner of the quadrat the colony of herbaceous plants included 7 *Bidens* seedlings, 1 clump of *Carex*, 3 clumps of *Juncus*, 9 *Rumex* seedlings, 3 flowering plants of *Senecio palustris*, and 9 *Typha* seedlings. Toward later summer this part of the quadrat became wholly covered with herbaceous vegetation in which *Typha latifolia* and *Juncus nodosus* were dominant species. There was a remarkable growth of the willow seedlings. In August the tallest measured over seven feet; the spreading stems transformed the thicket into a tangle of shrubs. Five species were noted among which *Salix longifolia* fruited, the second successional year. The others, were identified by foliage characters as *S. alba*, *S. lucida*, *S. missouriensis* and *S. pyrifolia*.

Because of the phenomenal development of the plant community during the summer of 1936 when competition between ecologically equivalent species was most pronounced, it became obvious that the quadrat method of study would give only a partial picture of the whole (fig. 2). Therefore, on June 30, a species count of the entire area was taken. Doubtful determinations were checked at later dates as the species flowered and fruited.

The zonal development of the vegetation pattern initiated in the pioneer stage, was sharply differentiated during the summer of 1936. The marsh merging into the bay on the west side was choked with growing plants dominated by *Typha* and *Scirpus validus*. Four other species of *Scirpus* were common. The societies of emergents included *Alisma subcordata*, two species of *Sagittaria*, vigorously growing colonies of *Carex*, *Elodea* and *Juncus*, each represented by several species. Among the eight species of grasses, *Agrostis stolonifera* formed dense, conspicuous mats in shallow water (fig. 3). In the zone of marsh vegetation six species of *Bidens* were floristically important components. They grew in masses covering acres of the area. Among them was *B. discoidea*, a coastal plain species which was smaller, more scattered and flowered earlier than the others.

The zone of willows extended through the center of the area from the northwest to southwest corners of the sand-fill bordering the marsh on the east side. Seedlings of *Populus balsamifera* were occasional in enclosures controlled by herbaceous species, including *Radicula palustris* and nine species of *Polygonum*. Like *Bidens* the latter grew in dense colonies spreading to the drier soil which supported many annuals.

The zone of annuals extended through the higher parts of the sand-fill between the zone of willows and Minnesota Avenue. Among the many species *Cycloloma atriplicifolium* and *Corispermum hyssopifolium* were predominant. *Erucastrum gallicum* was frequent, and there were rosettes of many biennials and seedlings of perennial *Compositae*. Mosses and lichens which were not identified formed an important ground covering in the moist soil under the willows, with *Equisetum arvense*, *E. laevigatum* and *Marchantia*

polymorpha. Thus, during the summer of 1936, the second successional year, over ninety species of flowering plants were growing in the area.

LIST OF SPECIES IN 1936

- Equisetum arvense* L.
E. laevigatum A. Br.
Typha latifolia L.
Alisma subcordata Raf.
Sagittaria arifolia Nutt.
S. latifolia Willd.
Agrostis alba L.
A. hymnalis (Wa't.) B. S. P.
A. stolonifera L.
Alopecurus aequalis Sobol.
Beckmannia syzigachne (Steud.) Fernald
Echinochloa crusgalli (L.) Beauv.
E. muricata (Michx.) Fernald
Glyceria grandis Wats.
Hordeum jubatum L.
Leersia oryzoides (L.) Sw.
Panicum capillare L.
Poa annua L.
P. triflora Gilib.
Carex bebbii Olney
C. scoparia Schkuhr.
C. crawfordii Fernald
C. cristatella Britton
C. projecta Moch.
C. vulpinoidea Michx.
Cyperus speciosus Vahl
Eleocharis acicularis (L.) R. & S.
E. ovata Roth.
E. palustris (L.) R. & S.
E. palustris (L.) R. & S. var. *major* Sonder
Scirpus atrocinctus Fernald
S. atrovirens Muhl.
S. cyperinus (L.) Kunth.
S. rubrotinctus Fernald
S. validus Vahl
Juncus alpinus Vill.
J. balticus Willd. var. *littoralis* Engelm.
Juncus balticus Willd. var. *littoralis* Engelm. f. *dissitiflorus* Engelm. ex Fernald
J. brachycephalus (Engelm.) Buchenau
J. bufonius L.
J. dudleyi Wiegand
J. nodosus L.
J. torreyi Coville
J. tenuis Willd.
Salix alba L.
S. longifolia Muhl.
S. lucida Muhl.
S. missouriensis Bebb.
S. pyrifolia Anders.
Populus balsamifera L.
Polygonum aviculare L.
P. acre H. B. K.
P. erectum L.
P. hydropiper L.
P. lapathifolium L.
P. persicaria L.
P. tomentosum Schrank
P. tenue Michx.
Rumex crispus L.
R. mexicanus Meisn.
R. persicarioides L.
Cycloloma atriplicifolium (Spreng.) Coult.
Chenopodium album L.
C. rubrum L.
Atriplex patula L.
Corispermum hyssopifolium L.
Salsola kali L. var. *tenuifolia* G. F. W. Mey
Amaranthus crispus (Lesp. & Thev.) A. Br.
A. retroflexus L.
Silene vulgaris Gaerck.
Ranunculus cymbalaria Pursh.
R. pennsylvanicus L. f.
R. sceleratus L.
Brassica alba Boiss.
ErUCAstrum gallicum (Willd.) Schulz
Lepidium apetalum Willd.
Radicula palustris Moench.
Sisymbrium altissimum L.
Penthorum sedoides L.
Euphorbia adenocaulon Haussk.
E. densum Raf.
Oenothera biennis L.
Mimulus ringens L.
Aster paniculatus Lam.
Bidens cernua L.
B. comosa (Gray) Wiegand
B. connata Muhl.
B. connata Muhl. var. *fallax* (Warnst.) Sherff.
B. connata Muhl. var. *pinnata* Wats.

B. discoidea (T. & G.) Britt.
B. frondosa L.
B. vulgaris Greene.
Eupatorium perfoliatum L.

Gnaphalium uliginosum L.
Senecio palustris L.
Solidago graminifolia (L.) Salish.

THIRD YEAR VEGETATION

In the spring of 1937, the third year of successional development, the trees within the quadrat were marked and recorded on a chart. Of 262 seedlings of the previous year, 170 developed. In later summer the tallest, *Salix longifolia*, were over fourteen feet high. The thicket was almost impenetrable (fig. 4). Unfortunately, the quadrat was laid out too close to the bay. In 1938, much of the sand-fill was flooded several inches deep. Wave action during high winds eroded much of the shore on the west side destroying vegetation including that of the quadrat.

The number of additional species migrating into the area during 1937 was surprisingly small. They were two species of *Potamogeton* which did not flower (*P. friesii* Rupr. and *P. richardsonii* (Benn.) Rydb.); *Scirpus debilis* L. and *Iris pseudacorus* L. The last was first collected in 1936 in a sedge meadow about one-half mile farther south. Obviously these plants are migrating across from the Wisconsin shore where the author during the past summer found a colony.

FOURTH YEAR VEGETATION.

During 1938, the fourth successional year, nineteen additional species were observed in the community. The floating aquatics were *Lemna minor* L., *Spirodela polyrrhiza* (L.) Schleid. and *Callitriche palustris* L.; the emergents included *Sium cicutaefolium* Schrank and *Sagittaria cuneata* Sheldon. The non-flowering aquatics, *Riccia fluitans* and *Spirogyra crassa* grew in abundance; at times the water was thick with colonies of *Nostoc*. About three-fourths of the additional species invading into the community in 1938, ecized in the drier soil of the zone populated by annuals. The seedlings of *Acer rubrum* and *Populus deltoides* were observed near the shore. The other new species were: *Phragmites maximus* (Forsk.) Chiov., *Juncus effusus* L. var. *pylaei* (Laharpe) F. & W., *Melilotus officinalis* (L.) Lam., *Trifolium hybridum* L., *Lycopus lucidus* Turcz., *Mentha canadensis* L., *Erigeron canadensis* L., *Helianthus annuus* L., *Solidago canadensis* L., *S. hispida* Muhl., *Sonchus arvensis* L., and *Taraxacum officinale* Weber.

PLANT MIGRATION

In the pioneer vegetation, wind-distributed types were predominant. A mass invasion of locally common species appeared to have taken place. This was obvious from the numerous *Salix* and *Typha* seedlings which had germinated in the area. The dominance of *Senecio palustris* lasted but a single

generation. After the first fruiting the plants were crowded out from the interior of the sand-fill by the spreading perennials. Consequently, the second germination took place on marginal shores still open to invasion.

Undoubtedly water played an important rôle in the migration of fruits and seeds adapted for floating, either by the small size or by some special device. The invading germules were further distributed by wave action within the sand-fill resulting in scattered families of several species which by vigorous growth merged together into a dense plant community. It is reasonable to assume that the miles of shoreline in St. Louis River and Bay, in Minnesota and Wisconsin formed the center of distribution. Most of the species in the community are known to occur locally. The presence of the few not known previously from the locality is problematic and is reserved for further investigation.

It is probable that the fruits of *Bidens*, naturally adapted for animal distribution were brought to the bare area by means of water. Two species fruited in the pioneer stage which resulted in aggregations. This, however, does not explain the masses of *Bidens* developing during the second year, which included four additional species and two varieties. Mass invasion was obvious, and it could not have taken place by means of animal life, because the locality is known to have only *Microtus pennsylvanicus* and *Lepus sylvaticus* in addition to the hundreds of shorebirds during spring and fall migration. The mammals were first observed in the area during the second year of development.

The occurrence of *Bidens discoidea*, a coastal plain species was significant. Previous to 1936, there is but one other known station of this species in the state. Dr. Norman C. Fassett collected it in 1926, near Winona along the Mississippi River, southeastern part of the state. *Erucastrum gallicum*, new to Minnesota, is not known to occur locally.

The probable presence of germules in the dredged soil was not investigated.

FLORISTIC CHANGES

The rate of the development of the plant community was at the maximum during 1936, the second successional year. Competition for space resulted in simplification of the floristic composition by elimination of less tolerant species, or in decrease of individual populations, first apparent in 1937. *Senecio palustris* dominated the pioneer stage but gradually decreased in numbers until it was hardly noticeable in the fourth year's succession. *Bidens discoidea* was common during the second year, but disappeared altogether in the fourth year's vegetation. The other species of *Bidens* played a prominent rôle in the community until 1938 when they were succeeded by *Typha*, *Scirpus validus*, and *Leersia oryzoides*. Consequently, the masses of these species covering large tracts of the area were reduced to a few individuals, frequently stunted and spindling in form. The species of *Polygonum* passed through similar reduc-

tion in population. They were succeeded by *Salix longifolia* and species of *Equisetum*. The annuals being succeeded by perennials were less frequent in the fourth year's growth. *Erucastrum gallicum* migrated to another sand-fill farther south. Other species no longer noted during 1938 were *Penthorum sedoides*, three species of *Ranunculus*, *Gnaphalium uliginosum* and *Minulus ringens*.

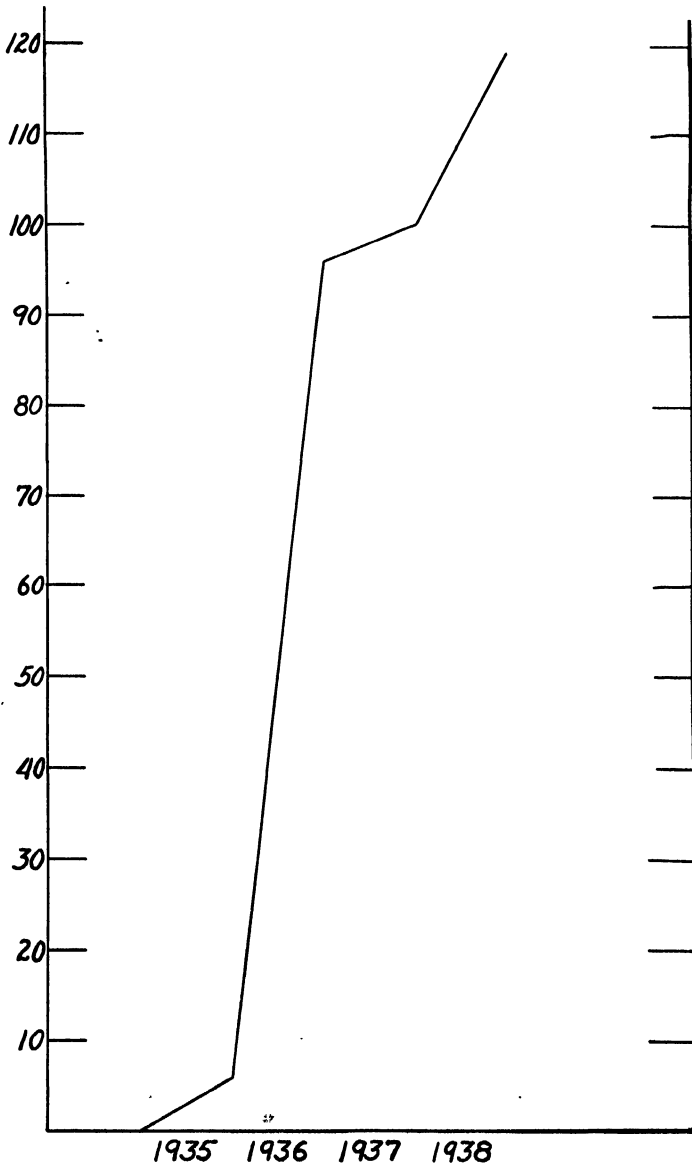


FIG. 6. Graph showing the invasion of species by years from the autumn of 1935.

In conclusion it may be stated that the rich silt content of the soil and the high water level promoted vigorous growth of marsh plants, dominated by *Typha* and *Scirpus validus* (fig. 5). The bare area lay open to plant invasion of many ecologically equivalent species which resulted in competition forming a dense willow thicket and a cat-tail marsh during four years of successional development. The greatest rate of change was manifested during the second year's growth when over eighty per cent of the total number of species were known to ecize in the area. Simplification by elimination was first apparent during the third year's growth. The tree succession will be carried on by *Acer rubrum* and *Populus deltoides*.

The flora included two notable coastal plain species, *Bidens discoidea* and *B. connata* var. *pinnata*. *Iris pseudacorus* and *Erucastrum gallicum* are new to Minnesota.

A complete list of the species is given as they invaded into the area during the four years of successional development (fig. 6).

The author wishes to extend thanks to Dr. W. S. Cooper, University of Minnesota, for suggestions in the study, and to the members of the botany classes of the State Teachers College who helped to record the quadrat populations.

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A COMPARATIVE STUDY OF THE ANIMAL POPULATION ON CERTAIN SUBMERGED AQUATIC PLANTS¹

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The importance of aquatic vegetation as a place of abode for aquatic animals has long been recognized and animal population studies of aquatic habitats have usually included at least some reference to the animals on the vegetation. It is quite generally recognized that the submerged, leafy types of vegetation are more densely populated than are the emergent, hard surfaced, non-leafy types, but exact and comprehensive quantitative or even qualitative information of a more specific nature is conspicuously meager.

Among the studies made on submerged vegetation are those of Moore ('13), Baker ('16, '18), Richardson ('21), and more recently those of the staff of the State of New York Conservation Commission including P. R. Needham ('28, '29), Pate ('32), Nevin and Townes ('35). Moore's observations were restricted to the potamogetons and were essentially qualitative, numbers being indicated by the general terms "abundant" and "scarce." Baker ('16), in his Oneida Lake studies on molluscs, made a closer approach to specific quantitative information by counting the molluscs on each leaf of each plant. Richardson ('21), using the general designation "weeds," made a quantitative examination of the upper nine inches of aquatic plants, the count being based on the animals which were washed off as the plants were shaken in water. In the studies carried on under the auspices of the State of New York Conservation Commission pure stands of submerged plants were designated but no distinction was made between the animals on the plants and those on the underlying substratum, and no attempt was made to determine the population on a plant by plant basis. There is thus clearly much room for precise information both with respect to the population of aquatic plants in general and with respect to given species of plants.

The results reported in this paper are based on a plant by plant examination of seven species of submerged, leafy aquatic plants, from the western region of Lake Erie, the examination being made with a view to determining both the composition and the quantity of the animal population. The plants were *Potamogeton compressus*, *Potamogeton pectinatus*, *Potamogeton crispus*, *Myriophyllum spicatum*, *Elodea canadensis*, *Najas flexilis*, and *Vallisneria spiralis* (Fig. 1). I am indebted to Prof. L. H. Tiffany for the identifications

¹ Contribution No. 16, from the Department of Zoology, Ohio University.

One of the primary requisites in a comparative study of this sort is that the plants compared be growing under essentially the same conditions. Otherwise the rôle of the plants as a responsible factor in accounting for such differences in the animal populations as may be observed cannot, readily, be

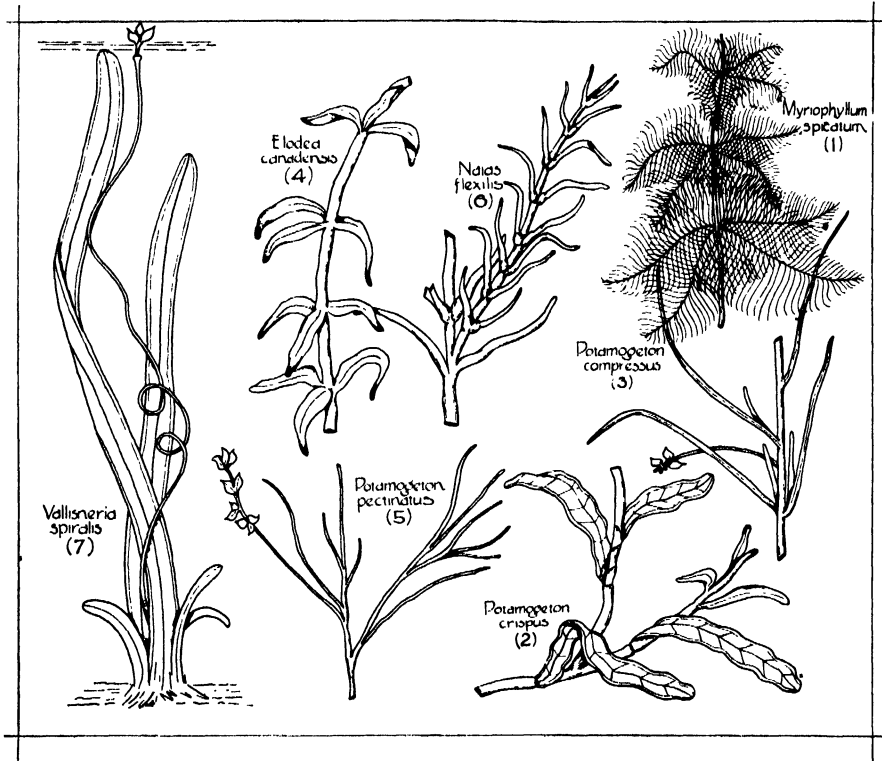


FIG. 1. The plants examined.

differentiated from the rôle of the environment. This uncertainty is one of the weaknesses in comparisons based on studies of pure stands, since, of course, two or more species of plants, each growing in a pure stand, are not necessarily growing under the same conditions. The requirements are obviously most nearly fulfilled when the plants to be compared are growing closely intermingled in a common bed of vegetation, and, thus, as nearly as possible under common environmental conditions. The plants selected for this study were chosen because they were thus growing together. Fortunately it so happens that they are among the more common species of aquatic plants. Beds of vegetation were selected in different sections of Put-in Bay Harbor, South Bass Island, Lake Erie (where the investigation was conducted during the summers of 1935 and 1936), and also in East Harbor, a marshy backwater on the neighboring mainland. In both of these regions dense mats of submerged vegetation grow on a muddy substratum protected from the agitation

of the open lake. In Put-in Bay Harbor, a bed of vegetation was examined in a section known as Squaw Harbor, another in the Hatchery Bay section, and a third in a row boat slip on Gibraltar Island.

METHODS

There is as yet no commonly accepted standard for comparing the population of one type of plant with that of another. In Baker's ('16) Oneida Lake study of molluscs, an entire plant was taken as the unit, all the animals on each plant having been counted. Accurate comparison by this method depends upon all plants being of the same size, a requirement which is difficult to fulfill and which Baker does not indicate was met. A more widely used but decidedly less precise method has been to express density of population in terms of the area covered by the plants examined. This method quite obviously does not lend itself to exact comparative studies since the number of plants is likely to vary in different areas. It is entirely inapplicable to a study in which the different plants to be compared grow in the same area.

In casting about for a more satisfactory basis of comparison it appeared that one depending upon linear feet of stem provides a criterion which can be applied to all plants regardless of their size and distribution and which can be based upon a single plant or upon parts of several plants of the same species as conditions make possible or desirable. In this study at least ten linear feet of each species of plant was examined from each of the situations in which the plant was found. In computing feet, branch growths more than an inch or two in length were not included in the unit being measured, but were treated as part of an additional foot. The particular number of feet was chosen rather arbitrarily, although it was influenced by the amount of plant which could be examined within a reasonable period and yet provide a surface area sufficiently large to furnish representative results. In most instances more than ten feet of a particular species was examined from a single locality in which case the results were reduced to a ten foot basis.

The plants were collected from a boat by reaching down into the water as far as possible and cutting off a single plant at a time. As the severed portion was lifted clear of the water, it was placed in a glass dish, a small amount of water was added and the dish was covered to prevent drying. Usually only as much plant was gathered as could be examined in the time immediately available so that all counts could be made while the animals were still alive. When it occasionally became necessary to continue the count at a later time, it was found that the animals could be kept in good condition in the laboratory from one day to the next, provided the vegetation was kept in a covered container so as to retain the moisture.

In the laboratory, sections of a plant were measured as needed. The leaves were clipped off into a petri dish containing water, the stalk was cut into inch lengths and the dish was then placed under a wide field binocular

for examination. The total number of feet of each species examined in this way depended upon the number of situations in which the species was found. Thus, over seventy feet each of *Myriophyllum* and of *Potamogeton crispus* were examined, forty feet of *Najas* and of *Elodea*, twenty feet of *Potamogeton pectinatus*, and ten feet each of *Potamogeton compressus* and *Vallisneria*.

The animals were identified to genera (in a few instances to order only, or to family, and nematodes to class), counted and recorded according to plant and locality for later analysis. Identification stopped short of species for several reasons among them, the method used in making the count. This was based on the fact that it is practically impossible to disentangle all the animals from the vegetation and that they are most easily found on the vegetation, while their own movements aid in discovering them. To have stopped for the examination of detail which in many instances is needed for species identification would have necessitated preserving the material and thus really defeating the end desired. Highly valuable as specific identification is, the order of events held in mind has been that it is first of all desirable to learn which plants are the most densely populated after which attention can be devoted to the specific character of the inhabitants.

THE ANIMAL POPULATION

The results have been analyzed in terms of the distribution of genera among the plants and also in terms of the frequency with which members of the respective genera occurred on a given plant.

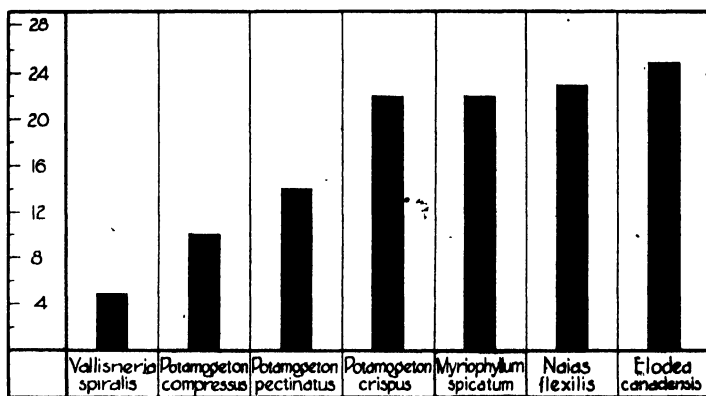


FIG. 2. Distribution of genera among the plants. The numerals on the left indicate the number of genera per plant.

Representatives of twenty-nine genera were found (Table I). Their distribution among the plants is graphically shown in figure 2, from which it will be seen that the number of genera per plant ranged from a maximum of 26 on *Elodea* to a minimum of 4 on *Vallisneria*.

An entirely different picture is presented when one compares the plants on the basis of the average number of individuals present on a ten foot length. In this case *Myriophyllum* with 1442 individuals and *Potamogeton crispus* with 1139 led all the others by a wide margin (Fig. 3).

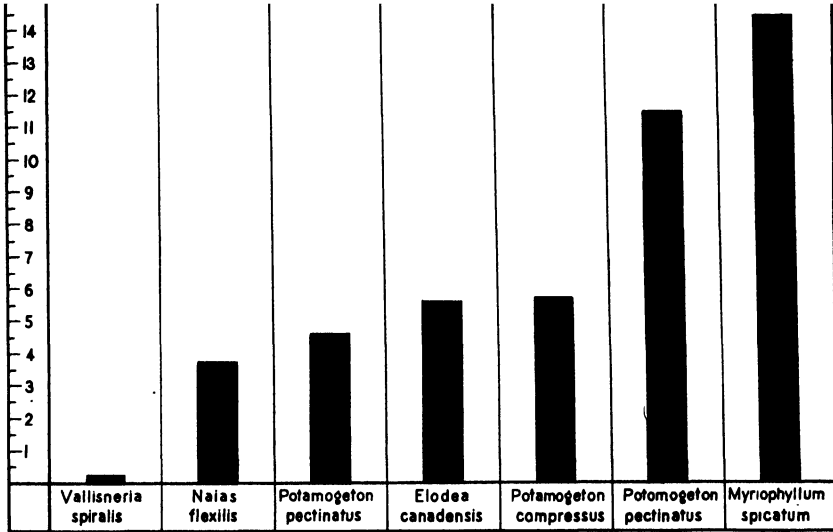


FIG. 3. The average animal population per ten feet of plant. The numerals on the left indicate the population in hundreds.

Average figures do not, of course, necessarily give a true picture of the distribution of numbers or of kinds of animals among the plants and cannot of themselves serve as an index of the suitability of one plant or another as a place of abode. Such suitability it was thought could be more clearly determined if a comparison were made based on the number of stations at which leading genera occurred on a plant and in addition on the number of stations at which a given plant was the most densely populated of the group. Since *Myriophyllum spicatum* and *Potamogeton crispus* completely outranked the other plants this comparison was limited to these two species. In considering their relative density of population, a comparison was made only when the animal in question was represented on both plants.

The results of the first comparison are graphically shown in figure 4. It will be seen that in eleven instances animals occurred on *Myriophyllum* but not on *Potamogeton crispus* and that in only four instances were animals on *Potamogeton crispus* but not on *Myriophyllum*, while in six instances animals occurred at the same number of stations on both plants.

With respect to the relative number of individuals on *Myriophyllum* and *Potamogeton crispus* a glance at figure 5 will show that in 25 instances a given animal was more abundant on *Myriophyllum* than on *Potamogeton crispus* at

a given station, whereas in only 13 instances was a given animal more abundant on *Potamogeton* than on *Myriophyllum*.

The number of individuals by which one plant exceeded the other at a given station ranged in the case of *Myriophyllum* (Fig. 6), from a majority of 10 in six instances through majorities of 20–40 in another set of six instances, 50–90 in eight cases, 100–400 in twelve cases up to a maximum of 1400 in

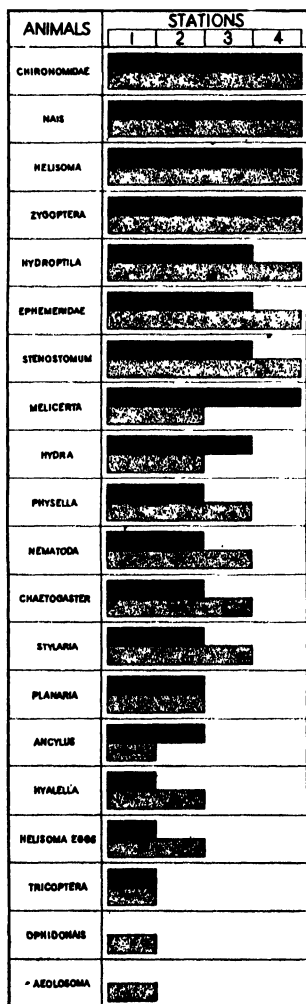


FIG. 4.

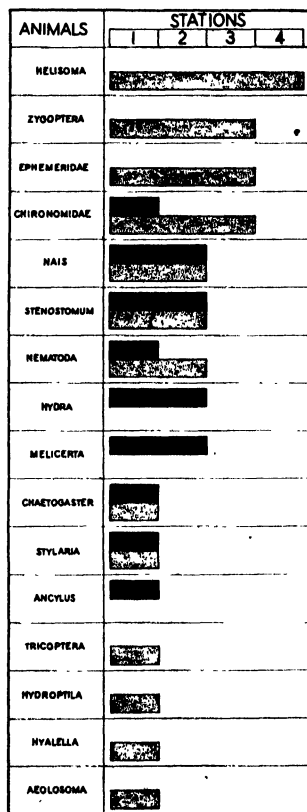


FIG. 5.

FIG. 4. Number of stations at which leading animals occurred on *Myriophyllum* and *Potamogeton crispus*. Black areas indicate *Potamogeton*, stippled areas *Myriophyllum*.

FIG. 5. Number of stations at which either *Myriophyllum* or *Potamogeton crispus* was the more densely populated by a given group of animals. Black areas indicate *Potamogeton*, stippled areas *Myriophyllum*.

TABLE I. Average and maximum population of ten linear feet of different species of plants
 The maximum number found on a ten foot length of plant is not on the same ten feet for all animals.

	<i>Elodea canadensis</i>		<i>Najas flexilis</i>		<i>Myriophyllum spicatum</i>		<i>Vallisneria spiralis</i>		<i>Potamogeton compressus</i>		<i>Potamogeton pectinatus</i>		<i>Potamogeton crispus</i>	
	Ave.	Max.	Ave.	Max.	Ave.	Max.	Ave.	Max.	Ave.	Max.	Ave.	Max.	Ave.	Max.
ANNELIDA														
<i>Aeolosoma</i>	1	1	3	13	2	16	—	—	—	—	—	—	—	—
<i>Chaetogaster</i>	5	8	8	31	26	166	—	—	17	17	6	9	19	70
<i>Dero</i>	2	8	—	—	—	—	—	—	—	—	—	—	1	6
<i>Nais</i>	40	111	169	323	435	1955	12	12	410	410	193	255	256	712
<i>Ophidonais</i>	—	—	—	—	17	120	—	—	—	—	—	—	—	—
<i>Stylaria</i>	34	93	19	73	90	228	—	—	2	2	5	10	37	181
Total	82		199		570		12		429		2 4		313	
ARTHROPODA														
Crustacea														
<i>Hyalella</i>	2	7	6	16	89	365	—	—	—	—	2	4	2	15
Total	2		6		89		—		—		2		2	
Insecta														
<i>Anisoptera</i>	1	2	—	—	1	1	—	—	—	—	—	—	1	1
<i>Chironomidae</i>	70	200	88	153	360	700	8	8	49	49	210	221	312	970
<i>Coleoptera</i>	1	1	1	2	—	—	—	—	—	—	—	—	5	30
<i>Ephemeridae</i>	1	1	21	70	63	260	—	—	—	—	3	3	3	11
<i>Hydroptila</i>	1	2	2	4	26	135	2	2	2	2	9	16	16	74
<i>Leptoceridae</i>	1	1	—	—	4	20	—	—	—	—	—	—	3	12
<i>Zygoptera</i>	15	30	11	27	64	200	—	—	4	4	6	8	16	43
Total	90		123		518		10		55		228		356	
MOLLUSCA														
<i>Ammicola</i>	—	—	—	—	1	3	—	—	—	—	—	—	—	—
<i>Ancylus</i>	4	10	1	2	2	7	—	—	—	—	—	—	20	96
<i>Goniobasis</i>	1	3	1	2	—	—	—	—	—	—	—	—	—	—
<i>Helisoma</i> p.	15	24	8	10	60	116	—	—	—	—	16	30	26	64
<i>Helisoma</i> e.	8	16	8	10	23	78	—	—	—	—	4	7	1	9
<i>Physella</i>	3	7	1	3	4	12	—	—	1	1	—	—	3	9
Total	31		19		90		—		1		20		50	
PLATHELMINTHES														
<i>Planaria</i>	12	26	5	10	23	110	—	—	—	—	2	2	21	80
<i>Stenostomum</i>	40	123	19	30	71	156	2	2	4	4	6	6	47	90
Total	52		24		94		2		4		8		68	
MISCELLANEOUS														
<i>Plumatella</i>	2	5	1	1	2	14	—	—	—	—	3	6	32	170
<i>Urnatella</i>	—	—	2	7	—	—	—	—	—	—	—	—	—	—
<i>Melicerta</i>	264	616	1	1	4	19	6	6	60	60	—	—	263	590
<i>Nematoda</i>	13	51	1	1	55	372	—	—	—	—	—	—	4	23
<i>Hydra</i>	22	50	4	6	20	67	—	—	15	15	3	4	50	172
<i>Spongilla</i>	1	3	—	—	—	—	—	—	—	—	—	—	—	—
Fish Eggs	5	20	1	5	—	—	—	—	—	—	1	1	—	—
Snail Eggs	—	—	—	—	—	—	—	—	8	8	—	—	1	1
Total	307		10		81		6		83		7		350	
Grand Total	564		381		1442		30		572		469		1139	

the single instance of *Nais*. The differences in favor of *Potamogeton crispus* were in general less, ranging from a majority of 10 in four instances through majorities of 20–60 in twelve cases, to maximum majorities of 180–290 in four instances for *Melicerta*.

Classes	Myriophyllum spicatum	Potamogeton crispus	Potamogeton compressus	Elodea canadensis	Potamogeton pectinatus	Najas flexilis	Vallisneria spiralis
Group Population	50 100 200 400	50 100 200	50 100 200	50 100	50 100 200 400	50 100	50 100 200 400
Oligochaeta	██████████	██████████	██████████	██████████	██████████	██████████	██████████
Crustacea	██████████	██████████	██████████	██████████	██████████	██████████	██████████
Insecta	██████████	██████████	██████████	██████████	██████████	██████████	██████████
Gastropoda	██████████	██████████	██████████	██████████	██████████	██████████	██████████
Turbellaria	██████████	██████████	██████████	██████████	██████████	██████████	██████████
Miscell....	██████████	██████████	██████████	██████████	██████████	██████████	██████████

FIG. 6. Analysis of the average population on each plant in terms of the taxonomic classes represented.

Details of the distribution of the various animals among the plants examined, their average numbers, and the maximum numbers of a given animal found at a single time and station are given in Table I. Among the interesting points brought out by this table is the fact that *Nais*, the Chironomidae, the larva of the caddis *Hydroptila*, and the flatworm *Stenostomum* were found on all the plants. The term *Stenostomum* here and elsewhere includes other rhabdocoels. Least widely distributed among the plants were the annelid, *Ophidonais*, the snail *Ammicola*, the bryozoan *Urnatella*, and the sponge *Spongilla*, each of which was found on only a single type of plant, and in some cases at only a single station. Another item of interest is the record that in one instance 1955 individuals of the small annelid, *Nais elinguis*, were found on a single ten foot length of the plant *Myriophyllum* and that on a ten foot length of *Potamogeton crispus* 970 chironomid midges were counted. *Nais* and the midges were with the exception of the rotifer, *Melicerta*, throughout the most abundant members of the population on each of the plants.

THE BASIS FOR POPULATION DIFFERENCES

The basis for the differences in density of population brought out by this study can with some assurance be looked for in the character of the plants rather than in the physical conditions of the environment since the plants always grew closely intermingled and hence under essentially similar environmental conditions.

Any one of several features might, of course, make a plant a favorable or an unfavorable place of abode. One of these is its chemical constitution although no data are available in this particular case and other features appear to be more directly involved. Some incidental observations indicate, however, that animals were not as abundant on unthrifty or decaying plants

as on those in good condition. The plants on which the population counts were made were all thrifty. The extent to which the morphological features of the plants appeared to afford protection and foothold showed some degree of correlation with their density of population. *Myriophyllum*, the optimum plant, has finely subdivided leaves (Fig. 1), which seem to be particularly well suited to the type of animals that occurred most abundantly on all the plants, namely, the annelids and midges. The midges were able to cling to such leaves with their hook-bearing appendages and the annelids could coil about them with ease. It is noteworthy, however, that most of the other animals also occurred in relatively large numbers on *Myriophyllum* (Table I). *Potamogeton crispus*, which is next in line, has a broad, unbroken leaf that is crenulated and often curled and thus fitted to provide favorable footing and protection. *Potamogeton compressus* and *Potamogeton pectinatus* have relatively slender, simple leaves. Both of these plants seem to provide rather favorable conditions for the annelid, *Nais*, while *P. pectinatus* also harbored a goodly number of midges. The leaves of *Naias* are likewise relatively slender. *Elodea* possesses broad, blunt leaves which are rather smooth and widely spaced. Neither the annelids nor the midges occurred on it in large numbers. It is interesting to observe, however, that both *Elodea* and the other broad-leaved plant *P. crispus* harbored the largest number of the sessile *Melicerta* and the semi-sessile *Hydra*. *Vallisneria*, the most sparsely populated plant of the group has smooth ribbon-like leaves which provide surface without protection.

CONCLUSIONS

In the foregoing paragraphs, the animal population of seven species of submerged aquatic plants has been described and analyzed on the basis of a plant by plant examination under the microscope. It was found that most of the taxonomic divisions considered (chiefly genera), were represented on each of the plants examined. It was quite obvious, however, that two of the plants, *Myriophyllum spicatum* and *Potamogeton crispus*, were by far more densely populated than the rest. Of these, four, *Naias flexilis*, *Potamogeton compressus*, *Potamogeton pectinatus*, and *Elodea canadensis* each harbored about the same number of animals. Still another plant, *Vallisneria spiralis* was entirely outclassed by all plants and harbored a negligible number of individuals. Actual numbers ranged from an average of 1442 individuals per ten linear feet of plant stem on *Myriophyllum* to a mere 30 on a similar length of *Vallisneria*. Midge larvae and freshwater annelids together made up from 59 per cent to 93 per cent of the population on all but one of the plants. On this one, which was *Elodea*, midges and annelids comprised 29 per cent of the individuals while the sessile rotifer, *Melicerta*, made up 50 per cent.

Practical fish culturists have long been concerned with learning what species of plants afford the best shelter and place of abode for the various

small animals which serve as food for young fish, and in some cases even older fish. The findings disclosed by this study point rather obviously to *Myriophyllum* and to *Potamogeton crispus* with special emphasis upon *Myriophyllum* since it led the *Potamogeton* in total average population for all localities examined as well as in the average population for most of the specific areas from which plants were taken. *Myriophyllum* also led in the number of animals which occurred on it in maximum numbers. Although only one species of *Myriophyllum* was examined, the structural similarities which exist between various species make it seem probable that the results would hold in the case of other species as well.

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PALaeoecology of a Central Washington Bog

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Pollen analysis has been made of a montane bog in the central part of Washington, about seven miles southwest of Wenatchee, in Chelan County. The bog lies at an elevation of about 4200 feet, and is located in T. 21 N., R. 19 E., in Sect. 12 on the Wenatchee Quadrangle. The apparent origin of the depression in which the bog has been developed is that of a landslide. Landslide lakes and depressions are conspicuous features in this area, and have resulted from slumping of receding basalt cliffs (Chappell, '36). There is no surface drainage outlet for the bog, but it probably has subterranean drainage. The area is in the Squilchuck drainage system, which drains directly into the Columbia River a few miles to the east. There is no evidence of mountain glaciation having occurred in the drainage system in which the bog lies. Apparently the divide was too low and the precipitation insufficient for the accumulation of snowfields. The bog comprises an area of perhaps two acres, and is covered with a dense stand of sedge (*Carex* sp.) and moss (*Hypnum* sp.), with scattered stands of *Eleocharis* sp. and *Alisma plantago-aquatica* where the surface has been disturbed. Near the margin of the bog there is a zone characterized chiefly by *Geum macrophyllum*, succeeded by zones of *Spiraea corymbosa*, *Cornus occidentalis*, and *Populus tremuloides*. The depth is four feet, with a *Carex-Hypnum* peat type throughout, underlain with fine, assorted sand.

The bog is within the Arid Transition (timbered) Life zone as defined by Merriam (1898). The forests adjacent to the bog consist almost entirely of western yellow pine, *Pinus ponderosa*, with a few Douglas fir, *Pseudotsuga mucronata*, western larch, *Larix occidentalis*, and lodgepole pine, *Pinus contorta*, present in the stand. Forest type maps of this area indicate a western yellow pine type of several size classes. Yellow pine is also climax in this area. Characteristic shrubs in this area include *Ceanothus sanguineus*, *Vaccinium membranaceum*, *Physocarpus malvaceus*, *Menziesia ferruginea*, *Pachistima myrsinites*, *Berberis repens*, and *Rosa gymnocarpa*. The Arid Transition gives way to the Canadian followed by the Hudsonian zone as the elevation to the west increases, while to the east and lower elevations it grades into the Arid Transition (timberless) zone (Piper, '06). Characteristic trees in the Canadian zone include western white pine, *Pinus monticola*, western hemlock, *Tsuga heterophylla*, white fir, *Abies grandis*, noble fir, *A. nobilis*, and Engelmann spruce, *Picea engelmanni*. In the Hudsonian zone sparse forests of sub-

alpine fir, *Abies lasiocarpa*, mountain hemlock, *Tsuga mertensiana*, Alaska cedar, *Chaemacyparis nootkatensis*, and white bark pine, *Pinus albicaulis*, exist. Both the Canadian and Hudsonian zones occupy narrow strips, the latter being confined to the ridge of the Wenatchee Mountains, the highest point of which is 6887 feet in this area. The above species are not confined entirely to their respective zones, of which in general they are indicators, but may extend into several adjacent zones depending upon the ecological conditions and stage of forest succession.

Samples were secured at six inch intervals with a Davis sampler, and the usual potassium hydrate method was used in the preparation of slides for study. Two hundred or more pollen grains were identified from each level.

AGE OF THE BOG

It is not possible to employ the usual method of dating the bog, because no late Pleistocene glaciation has occurred in the vicinity, and the depression does not owe its origin to glaciation. A landslide may occur at any time, and while four feet of peat probably indicates the elapse of several thousand years for its deposition, it is difficult to even make an estimate. An inch layer of volcanic ash at the 3 foot level may be correlated with ash in other bogs in the Pacific Northwest which are of Wisconsin age. In diagrams of profiles of bogs in the Puget Sound Basin, Rigg, '38, shows the position of the ash. When the ash occurs it is found below the half-way level, with an average of about one-fourth of the peat below and three-fourths above. Pollen analysis of two bogs in the Puget Sound region shows that the deposition of peat began soon after the recession of the last ice-sheet (Hansen, '38). In a bog near Spokane, Washington, the ash layer is about one-third the distance from the bottom, and in a northern Idaho bog, it occurs one-fourth the distance from the bottom. The ash in the bog of this study seems to be about in the same relative position with respect to the depth of the peat. If the ash came from the same eruption, which is possible as there is one layer, it would indicate that the Wenatchee bog is older than the thickness of the peat would indicate. It may have had its origin soon after the retreat of the last ice-sheet.

The peat is strongly compressed and homogeneous in texture and composition throughout most of its depth. Time estimates have been made for the accumulation of one foot of peat, with considerable differences in opinions by the investigators (Sears, '33). Sears estimates about 300 years for the accumulation of a foot of peat in Ohio. In the bog of this study, peat accumulation has probably been very slow, because of the semi-arid climate, and the fact that most of the precipitation occurs in the non-growing season. Lesqueux (1885) estimates that peat in the lower levels may be compressed to less than one-eighth of its original volume, but this would depend upon the depth of the deposit and its composition. Taking these facts into consideration, it is estimated that the peat deposit has required 4000 years for its time of accumulation.

SIGNIFICANCE AND CORRELATION OF THE POLLEN SPECTRA

In studying forest succession in a montane region, based upon pollen analysis, one must consider the proximity of several life zones to the bog. The bog in its development may receive pollens from higher and lower zones as well as from the one in which it is situated. The percentages of pollens of different species, however, should indicate the relative abundance and nearness of the trees, and give a fairly accurate picture of forest succession. Overlapping will be shown as succession takes place because of climatic change. The occurrence of a species in several life zones adds to the complexities of the problem.

Bogs which have developed in depressions and lakes associated with glacial recession record primary forest succession generally conceded as having begun in denuded areas. In the bog of this study the lowest level shows yellow pine to have a frequency of 12 per cent, grass 15, lodgepole pine 17, and white pine 27 per cent (fig. 1, table I). The first two possibly indicate that a somewhat

TABLE I. *Percentages of principal pollens*

Depth in feet	4	3.5	3	2.5	2	1.5	1	0.5	S
<i>Pinus contorta</i>	17	7	8	12	10	3	6	3	5
<i>P. ponderosa</i>	12	6	5	17	25	29	37	50	56
<i>P. monticola</i>	27	15	15	30	19	18	14	4	3
<i>Pseudotsuga mucronata</i>	4	30	28	15	17	18	15	12	7
<i>Larix occidentalis</i>	1	7	10	3	5	3	4	4	4
<i>Abies grandis</i>	5	0.5	1	2	1	2	1	1.5	2
<i>A. lasiocarpa</i>	0.5		1	2	4	1	2	0.5	
<i>Tsuga heterophylla</i>				1	1	0.5	2	1	1
Gramineae	15	23	22	13	15	17	13	20	15
<i>Acer</i>	10	5	5	2	0.5	1	1	2	1
<i>Alnus</i>	7	4	2	2	1	5	3	1	2
<i>Salix</i>		0.5	2	0.5	1			0.5	
<i>Betula</i>	1		0.5				0.5		
Compositae		1	1	0.5			1	1	3
Chenopodiaceae		1	1		0.5		1	0.5	
<i>Typha</i> *	8	7	13						
Sedge*	6	3	40	67	72	88	53	31	11
<i>Nymphaea polysepala</i> *	2								

* Number and not computed in the percentages.

warm and dry period had already been reached at the time of initiation of the bog. In a region supporting a yellow pine climax, it is evident from previous study that the initial forests to invade a recently deglaciated region consist of species which thrive in cooler climate. A bog situated near Spokane, Washington, in a yellow pine climax, shows no trace of this species in the lower two levels (Hansen, '39). When it does appear as recorded by its pollens it shows a rapid and constant increase to over 40 per cent at the surface. Lodgepole is the dominant pioneer species with high frequencies in the lower levels. The origin of this bog is correlated with the retreat of ice of Wisconsin age and it probably records the postglacial history of yellow pine in that region. Bogs

in the Puget Sound region and one in Northern Idaho also show a preponderance of lodgepole pine in the lower levels (Hansen, '38, '39). In view of these data, it is evident that some postglacial time had elapsed before the origin of the bog. The presence of Canadian and Hudsonian zone species indicates a cooler climate than exists at present.

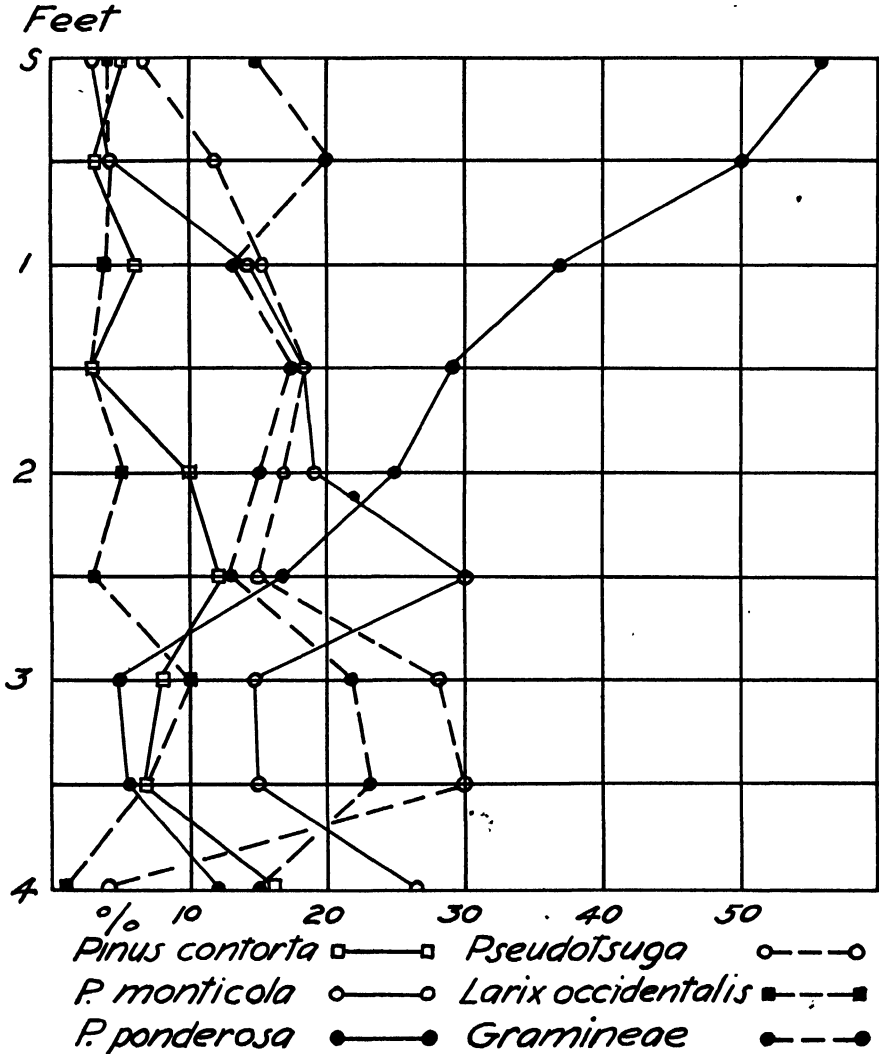


FIG. 1. Pollen diagram for a Washington bog.

The decrease in the frequencies of yellow, lodgepole, and white pines at the 3 foot level, and the sharp increase in Douglas fir may point to a brief period of warming, during which the less tolerant yellow and lodgepole pines were replaced to some extent. This same period of warmth which occurred

before the deposition of volcanic ash, is more definitely reflected in the bogs near Spokane and northern Idaho. The increase in grass and larch may indicate fire, in which case grass and the fire-resistant larch would increase for a time. Larch is resistant to fire because of its thick bark, and becomes more abundant after severe fires (Larsen, '29).

Increases in the frequencies of yellow, lodgepole, and white pines at the 2.5 foot level may indicate desiccation or a resumption of normal plant succession after the effects of the fire had been modified. The continued and constant increase of yellow pine to 56 per cent at the surface, and the decrease in Douglas fir marks the continued cooling of the climate to the present time. The decrease in white and lodgepole pines, probably records their migration to higher elevations. The constant frequencies of grass tend to show its normal abundance in the yellow pine climax. At the surface are found the following percentages: yellow pine 56, grass 15, Douglas fir 7, lodgepole pine 5, larch 4, and white pine 3 (table I). If an abundance count were made in this area, the above species might well occur in these proportions.

SUMMARY

The critical and best indicator species of this study seems to be western yellow pine. It probably records a gradual cooling and drying of the climate, from 3 feet to the surface.

Lodgepole pine which was a pioneer invader in the Puget Sound region, in Northern Idaho, and in the vicinity of Spokane, was never abundant and shows a general decrease from the bottom to the surface. The high frequencies of Douglas fir in the lower levels may record a warmer period, while its decrease marks drying and cooling, as does likewise the decrease in larch and white pine. The tolerance of conifers for shade is an important factor, and forest succession in the Northwest is perhaps dependent more upon their shade enduring relationships than upon climate. Yellow pine is the least tolerant, followed by larch, lodgepole pine, Douglas fir, and white pine.

White fir, subalpine fir, and hemlock pollens are present in small percentages throughout most of the bog. These likely found their way into the bog from higher elevations. Apparently the Canadian and Hudsonian zones shifted to higher elevations during the time represented by the peat deposit. The age of the bog is indefinite, but upon the basis of the indicated forest succession, it originated after some postglacial time had passed.

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ECOLOGICAL DEPTH-TEMPERATURE AREAS OF BENTHOS MASS-FORMS OF THE BARENTS SEA

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INTRODUCTION

Collections of quantitative material concerning the benthos distribution of the Barents Sea were made for a period of ten years (1924–1933) upon the research steamer “Persey” of the State Oceanographical Institute, by means of Petersen’s bottom sampler. Altogether about 500 stations were made. They were distributed rather unevenly in the open parts of the Barents Sea which occupies an area of about 1.3 million square kilometers.

Apart from the main problems of this ten-year investigation work, which were published by a number of authors (L. A. Zenkewitch, V. Brotzky, M. Idelson and R. Leibson) in a series of articles it seemed of interest to attempt to draw some conclusions of an ecological nature from this vast quantitative material.

ECOLOGICAL TEMPERATURE AREAS

One of our aims was to determine what factors are associated with the accumulation of the greatest quantities of the various benthos forms, *i.e.* their biomass.

The Barents Sea, while occupying a rather large area, represents a shallow, epicontinental basin with depths rarely exceeding 400 meters. With regard to temperature, there are slight variations between 8° and -2° C., with comparatively small seasonal changes in the near-bottom parts of the sea. The warmest portion of the sea is its south-western part, the coldest—its northern and eastern parts.

For analysis of the leading forms of benthos we used the following method in the present work: a graph was drawn upon the abscissa of which were plotted all the temperatures (from 8° to -2°) occurring in the near-bottom layers of the Barents Sea. Upon the ordinate of this graph were plotted all the depths (0–100; 100–200; 200–300; 300–400; 400–500 meters) found in the Barents Sea. Thus we obtained a kind of diagram (grate-like), covering these two factors and reflecting their variation within the limits of the Barents Sea. Each square of the diagram corresponds to a certain temperature-depth combination. For each mass benthos form we filled in the diagram in the following manner: all the data concerning the biomass, corresponding

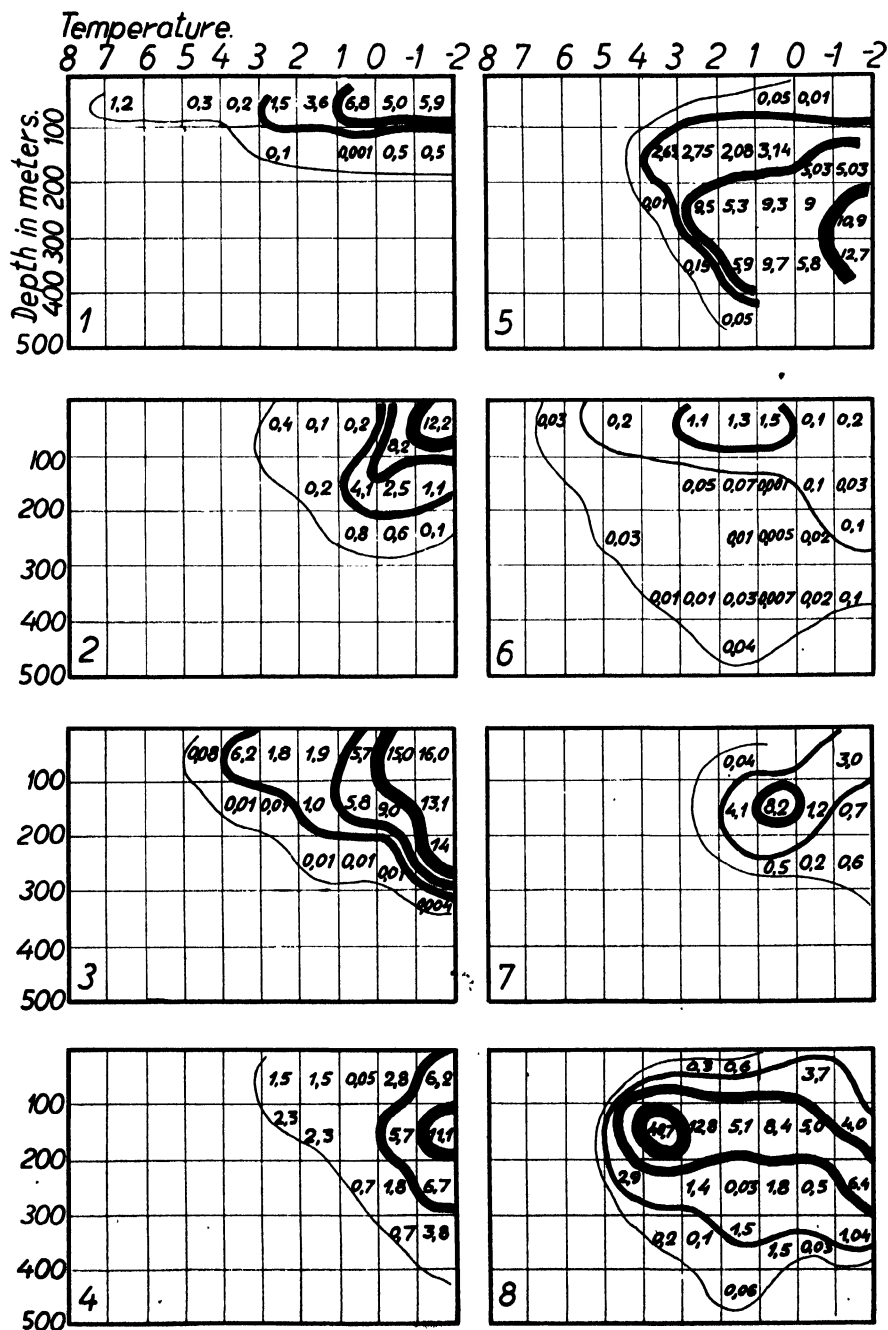


FIG. 1. Ecological areas for: 1. *Pelonaia corrugata*, 2. *Astarte montagui*, 3. *Macoma calcarea*, 4. *Phascolosoma margaritaceum*, 5. *Spirochaetopterus typicus*, 6. *Owenia assimilis*, 7. *Astarte elliptica*, 8. *Astarte crenata*.

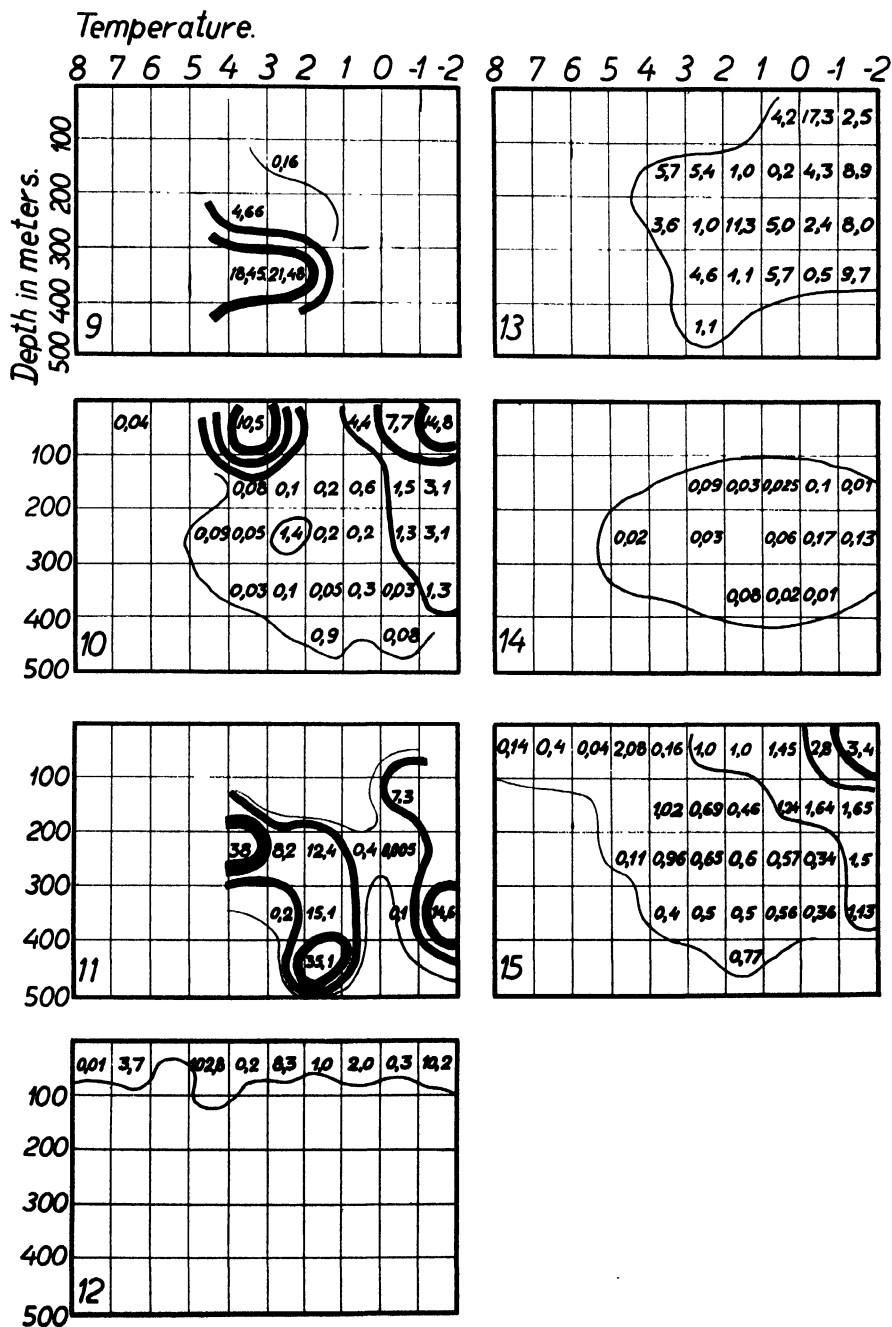


FIG. 2. Ecological areas for: 9. *Brisaster fragilis*, 10. *Maldane sarsi*, 11. *Molpadia* sp., 12. *Cardium groenlandicum*, 13. *Ctenodiscus crispatus*, 14. *Portlandia lenticula*, 15. Average ecological areal for all the 50 mass-forms.

to a certain depth and temperature all over the sea, is entered in a separate square. The figures shown in the graphs (Figs. 1, 2) are mathematical averages calculated from the data pertaining to each square.

On the basis of these averages it is possible to draw isolines for identical biomass and to show upon the graph the adaptability of the biomass of various forms to certain conditions. Other authors have also used graphical methods in ecological work similar to the one described (Pierce, '16; Parker, '30; Sweetman, '31). Several ecological areals of the mass benthos forms of the Barents Sea are shown in figures 1 and 2.

By examining the diagrams, it becomes apparent that several basic, typical groups may be distinguished. However, before touching upon them, we consider it necessary to point out the following two points in order to avoid misinterpretation of the material.

First, the whole of the material investigated has been collected by the Petersen's bottom sampler, hence it is affected by all the advantages and disadvantages connected with this instrument. While, for a number of forms we gathered valuable quantitative material impossible to obtain by any other means available to the biologist, there are some other forms which either escape the bottom sampler altogether or are not fully represented by the material obtained therewith. Thus the 50 mass benthos forms we were studying do not really include all the mass benthos forms actually existing in the Barents Sea. This is also evidenced by the systematic composition of our mass forms.

Kind of form	Number
Lamellibranchiata	16
Echinodermata	14
Polychaeta	17
Bryozoa	1
Ascidia	1
Sipunculidae	1

The materials collected by means of the bottom sampler fail in the main to give a true representation of (1) the very mobile forms and (2) of both the mobile and the sessile forms of patchy distribution. However, we are justified in believing that the 50 forms investigated by us represent more than half of the actual list of mass benthos forms existing in the Barents Sea.

Second, in the following discussion the boundary of an area, especially in its application to the graphs representing the ecological areas, is to be understood conditionally. It must be borne in mind that, as the material we were working with was collected by means of the bottom sampler, one or another of the forms might probably occur beyond the limits of the area indicated on the graph, but at such a degree of dispersion that it was not indicated in the bottom sampler collections.

The figures in the graphs (Figs. 1, 2) correspond to the average biomass of the given form in grams per square meter.

In studying the graphs of the ecological areas, it must be remembered that the bottom left corner of the graph does not give a true reflection of the temperature-depth relation in the Barents Sea. A temperature over 4° C. at a depth below 100 meters is practically non-existent in the Barents Sea, although there are corresponding squares on our graphs. Conditions corresponding to the bottom right squares of our graphs, *i.e.* a temperature below zero at depths deeper than 400 m. do not actually exist either. It is furthermore to be noted that the materials under consideration do not include the shallowest portion of the sea—its littoral zone.

CENTERED AREAS

Forms showing a distinct center of the ecological area to which the largest biomass accumulations are adapted (about 75 per cent of our mass forms) may be called *Centered Areas*. In these the center of mass accumulation is generally situated, not in the center of the ecological areal, but eccentrically and the areas are monocentric in the prevailing majority of cases. Among the forms with monocentric centered areas may be distinguished the following:

1. Shallow-water forms with accumulations in the coldest portion of their distribution but extending also to the warmer shallow-water regions. *Pelonaia corrugata* (Ascidia) may serve as an example of this type (Fig. 1—1). Also *Yoldia hyperborca* among the bivalve molluscs, *Ophiura nodosa* among the echinoderms and *Owenia assimilis* and *Lysippe labiata* among the Polychaeta have the same kind of area. This group composes about 12 per cent of the forms investigated.

2. Of still greater importance in the fauna of the Barents Sea are the forms of which the center of mass accumulation is located in the coldest and shallowest portions of the sea, their areas, however, covering greater depths by expansion. About 25 per cent of the mass forms examined belong to this group. In these cases the center of the area is either pressed into the very corner of the diagram, in the case of the mollusc *Astarte montagui* (Fig. 1—2) and also in a number of other forms (*Astarte borealis* and *Cardium ciliatum* of the molluscs and *Terebellides strömi* and *Rhodine gracilior* of the Polychaeta) or is lowered to a depth of 200–300 meters, as in the case of the mollusc *Macoma calcarea* (Fig. 1—3). Similar areas belong to the molluscs *Leda pernula* and *Nucula tenuis*, to *Psolus phantapus*, *Ophiura robusta*, *Ophiocten sericeum* and *Ophiopholis aculeata* of the echinoderms and to *Thelepus circinnatus* of the Polychaeta.

3. By some single forms the center of area falls upon the coldest regions of the medium depths, as for example in the case of *Gephyrea Phascolosoma margaritaceum* (Fig. 1—4).

4. A fairly large group of the mass forms (about 15 per cent) lowers the center of area to the greatest depths of the Barents Sea, keeping to the coldest

zone. The Polychaeta *Spiochaetopterus typicus* (Fig. 1—5) may serve as an example of this type. A similar area belongs to the molluscs *Arca glacialis* and *Portlandia intermedia*, the echinoderm *Ophiopleura borealis* and the polychaetes *Myriochele oculata* and *Onuphis conchylega*. Thus 52 per cent of all the mass forms investigated are to be found among those in which the center of area is located in the coldest zone. An extreme case of this type of area is afforded by the mollusc *Portlandia arctica* by its adaptability to the lowest temperatures, dwelling the whole year round at an almost constant temperature of about -2° C. in the deep furrows of the south-eastern part of the Barents Sea.

The next groups remove the center of their areas from the right margin of the graph, shifting it to the warmer parts of the sea.

5. A few of the mass forms of our collection like *Owenia assimilis* (Fig. 1—6) retain the center of area in the shallow water zone, while shifting it to the warmer regions of the sea.

6. A somewhat greater number of forms, such as the mollusc *Astarte elliptica* (Fig. 1—7), the brittlestar *Ophiura sarsi* and the polychaete *Lumbriconereis fragilis*, for instance, have the center of their area situated at the medium depths. The center of area of *Astarte crenata* (Fig. 1—8) is removed still further to the left side.

7. A small number of forms have the center of area in the western, warmest part of the sea and do not expand to the east. Among the mass forms of our collection, the irregular sea urchin *Brisaster fragilis* (Fig. 2—9) and the polychaete *Asychis biceps* belong to this group.

8. There are furthermore some forms that show a polycentrical area which we are inclined to attribute to the heterogeneity of the material. In such cases we apparently are involved either with ecologically different species or with smaller taxonomical units, like the polychaete *Maldane sarsi*, for instance (Fig. 2—10). The presence of at least two races is indicated by its ecological area. Similar polycentrical areas are formed also by the polychaete *Scoloplos armiger* and by the Bryozoan *Alcyonidium disciforme*. By way of comparison we may mention the ecological area of the holothurian *Molpadia* sp. (Fig. 2—11), the systematic heterogeneity of which is well known in the Barents Sea.

ACENTRICAL AREAS

Forms failing to show a distinct center of ecological area are referred to as *Acentrical Areas*.

A comparatively small number of forms—12 in all, or 25 per cent of the mass-forms investigated—belong to this type. These can also be sub-divided into groups in the same manner as the previous ones, namely:

1. Shallow water forms prevailing in the colder parts of the sea, such as *Cardium groenlandicum* (Fig. 2—12). Similar areas are produced by

two other shallow-water forms—the polychaetes *Travisia forbesi* and *Ophelia limacina*.

2. A considerably larger group of forms, like the star *Ctenodiscus crispatus* (Fig. 2—13), for instance, occupies the still colder regions of the sea. The molluscs *Axinus flexuosus* and *Chactoderma nitidulum*, the echinoderms *Ophiocantha bidentata*, *Trochoderma elegans* and *Strongylocentrotus droebachiensis* and the polychaete *Pectinaria hyperborea* have the same kind of areas.

3. Some forms with acentric areas are removed from the extremely cold right margin of the graph and are distributed in its middle part. The mollusc *Portlandia lenticula* (Fig. 2—14) and the polychaetes *Praxillella affinis* and *Praxillella gracilis* belong to this type.

Thus both the centered and acentric areas show the same (parallel) basic lines of territorial changes with the only difference that the areas of some forms form a center with a gradual decrease of population density towards the periphery, while the areas of others do not. Why some forms occur almost everywhere in a region under review, giving always a small but sometimes very stable biomass, while others are found in small quantities in some parts of the area and in large mass accumulations in others, no explanation can yet be offered.

This eccentricity in the population density of a form is apparently connected with the fluctuating dynamics of the area itself. We are aware that in periods of known duration considerable changes take place in the thermal characteristics of the different parts of the sea. However, of still greater importance are the more permanent climatic changes during the last thousands of years which are taking place at the Barents Sea as a part of the Polar Basin. According to many authors, the Barents Sea is undergoing a climatic change. If we assume that the climate of the Barents Sea is becoming colder, how are we then to interpret the ecological areas under review? In order to make this clear, we drew an average ecological area (Fig. 2—15) on the basis of the 50 graphs obtained for the different mass-forms. The obtained graph shows a fairly steady decrease of the average biomass, beginning at the shallowest and coldest corner of the sea. If we accept the supposition of a gradual cooling of the Barents Sea, such a distribution of the biomass of the Barents Sea mass forms seems incomprehensible, unless we assume that this increase in the biomass is due to new immigrations into the Barents Sea of the highly arctic forms from the North and the East. However, such an explanation is at variance with our knowledge of the bottom fauna of the Barents Sea. It would not be clear in that case why the prevailing majority of the Barents Sea mass forms keep so closely pressed to the coldest region of the sea. It is of importance in this respect to consider the nature of construction of the majority of the areals examined.

Let us take, for example, the ecological areas of *Astarte montagui* (Fig. 1—2) and of *Phascolosoma margaritaceum* (Fig. 1—4). Being pressed to

the very coldest region of the sea, these areas form graphically something like the left half of a normal area. As regards the right half, there is and could be none, because there is no temperature in the sea below -2° C. Such areas are apparently formed in the course of struggle for existence by the occurrence of ecological mutations and subsequent natural selection. Within the range of the ecological areas obtained there can be distinguished separate zones within each area. H. Broch ('33) gives an analysis of a geographical area within which he distinguishes two zones—the normal area (*Normalareal*) and the tolerance area (*Toleranzareal*) and their corresponding margins—the regional (*regionale Grenze*) and the tolerance margin (*Toleranzgrenze*). Besides these, one may further make use of the conception "*Kümmeregion*" introduced by Remane ('34). In general, we consider it advisable to divide the ecological area (and withal the geographical one) into zones in the following manner:

1. *The Center of Area*—a comparatively small region to which the extremely high accumulations of a form are adapted. It may be situated either in the geometrical center of an area or eccentrically.

2. *The Main Zone*—a fairly large region where the form is generally present and favorable conditions exist.

3. *The Tolerance Zone*—a region where the form, though present, does not attain sufficient development.

4. *The Depressive Zone (Kümmersonne)*—a region where the form though existent, is in a markedly depressed state (dwarfishness, retarded reproduction, etc.).

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REVIEWS

SWISS FOSSIL POLLEN ANALYSIS ¹

The Sihl valley moor of the canton Schwyz extends from the junction of the Minster and Sihl rivers to the village of Schlagen, a distance of nine and one half kilometers. During the retreat of the glacier which covered this area, a large glacial lake existed between the edge of the ice and the terminal moraine east of Einsiedeln. Subsequent to the drainage of this lake, the formation of the moor began with the deposition of marl at the union of the Minster and Sihl rivers. In some localities the marl exceeds a depth of sixty meters. The peat in general is lacking in macroscopic remnants of trees and shrubs, *Pinus*, *Picea*, *Betula* and *Alnus* are reported to have been found in a few places. Peat was collected at many stations located on a line running in a north-south direction. The pollen analyses show that there was a succession of forests during the development of the moor and the dominant trees from early to recent times were as follows: Pine (Palaeolithic) → Pine-Hazel (Mesolithic) → Hazel-mixed oak (Mesolithic) → Fir (Neolithic) → Fir-spruce (Neolithic) → Fir-spruce-beech (Bronze) → Spruce-pine. *Tilia cordata* was common during the hazel-mixed oak period.

From the results of this investigation it is interesting to note that due to the proximity of the mountains to the northern part of the moor, the hazel-mixed oak period in that section was shorter in duration than the southern. *Fagus* pollen were also less abundant in the northern part.

JOHN VOSS

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NEW ZEALAND FOSSIL POLLEN ANALYSES ²

The use of fossil pollen statistics in a region so far removed from the glaciated areas of the North Temperate of Europe and America as New Zealand is worthy of notice. Miss Cranwell has overcome the tremendous handicaps of such investigations in a region where neither the peats nor the pollens are known. Her pollen diagrams from six localities illustrate the percentage occurrence of four climatically significant groups: (1) The podocarps: *Podocarpus totara*, *P. ferrugineus*—*P. spicatus*, *P. dacrydioides*, *Dacrydium*, and *Phyllocladus* groups. (2) The beeches: (a) The *Nothofagus*

¹ Lüdi, Werner. 1939. Die Geschichte der Moore des Sihltales bei Einsiedeln. *Geobot. Inst. Rübel in Zürich*.

² Cranwell, L. M. 1938. Fossil pollens. The key to the vegetation of the past. *New Zealand Jour. Sci. Tech.* 19: 628-645, 9 fig.

Menziesii, and (b) the *Nothofagus* spp. types. (3) Southern rata, *Metrosideros umbellata*. (4) Grasses and sedges.

The diagrams are interpreted as follows: (1) Grassland period; final stages of the last period of glaciation, severe climate with slight regional differences only; (2) Podocarp forest period; uniformly wet and, probably, warm climate; (3) *Nothofagus* forest and grassland mosaic period; deterioration of the climate, distinct differentiation into local climate districts.

The author promises future work to show the degree of warmth of Period 2, a description of New Zealand pollen, and field work in the Auckland Province.

S. A. CAIN

LEAVES AND STEMS FROM FOSSIL FORESTS¹

The extensive coal fields of Illinois are especially rich in fossil plant material. The "Mazon Creek Region" provides such an abundance of leaves and stems of past ages that from it the vegetation of the coal measures has been visualized and reproduced in a remarkable museum group depicting the carboniferous forest. This manual describes in non-technical but scientifically accurate terms many of the fossil remains that went to form such a forest and are now preserved in the State Museum largely in the remarkable Langford Collection.

The specimens are made more interesting and intelligible by descriptions of the methods employed in obtaining the fossils from concretions abounding in the shale heaps following coal mining operations. This leads naturally to a consideration of various types of fossils and the processes of fossilization. Methods of fossil study include the reconstruction of the plant from the fragments and of the forests from the plants. Hardest of all is visualization of the ecological conditions under which coal grew reproduced and passed away.

Glimpses of all these things, well illustrated by excellent photographs of fine museum specimens, come to the reader of this interesting volume that has an appeal to the man on the street, to the ecologist and to the paleontologist.

GEO. D. FULLER

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A SCIENCE DICTIONARY²

Various, not too successful, attempts have been made to compile botanical or zoological German-English dictionaries but this seems to be the first time that such a handbook has been attempted for both biological and physical

¹ Janssen, Raymond E. 1939. Leaves and stems from fossil forests. *Illinois State Museum, Pop. Sci. Se. 1*: 1-190. 165 fig. Springfield, Illinois. \$1.50.

² De Vries, Louis. 1939. German-English Science Dictionary for Students in the Biological, Agricultural and Physical Sciences. x + 473 p. McGraw-Hill Book Company, Inc. New York. \$3.00.

sciences. The results are most promising although only prolonged use will answer the final question of successful accomplishment. A list of over thirty scientists who have collaborated with the author, who is a professor of modern languages at Iowa State College, speaks for the thoroughness of the work of preparation. It has successfully passed the tests that the reviewer has made in the botanical field.

The relatively small but clear readable Roman type has brought its 48,000 entries within the scope of 473 pages of pocket size. The thin paper and semi-flexible covers have made the volume convenient for easy reference. Special attention seems to have been given to short root-stems so much used in the composite words so abundant in the German language.

A brief appendix of abbreviations commonly used in science with their German and English equivalents is sure to be found useful. On the whole it seems certain that graduate students, and many of their instructors, seeking a reading knowledge of scientific German will find this book a most efficient aid.

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NOTES AND COMMENT

THE MOUNTAIN LION AND ECOLOGY

The ever-increasing clamor against the predators is a hue and cry which the ecologist might well hearken to. It is a complaint which is sketched along purely ecological lines but which is fostered and abetted by few who have ever heard the word "ecology." Predators have earned the enmity of man because they are purportedly out of step with modern ecology; balance, it is usually termed, but those who seek to right the balance must recognize the properties, interrelations, and reactions of the balance factors. * Rather few of the experts in wild life control or management have gone beyond the medieval "because of this result, this cause is responsible" mode of thought. Nor does the predator problem stand by itself as any good naturalist can testify. Floral complexes as well as animal problems are directly connected with the predator situation and indirectly, of course, geological and economic factors as well.

The mountain lion, especially in the western portion of North America, as being the largest and most romantic of our predators, has received attention second only perhaps to the coyote. This attention has been for the most part that of the game and stock interests who sought to exterminate the lion wherever found and under whatever conditions. This tradition is, of course, no new thing. No one will deny that man, as the superpredator, has become an ecological factor himself. Few killing factors are as important a predator as the rifle. The fight on the predators is an attempt to fit ourselves into a picture which was near complete without us. Any premise which may be supported by a modern ecologist must be founded upon the above basis and include the human with the other predators. No ecological picture is complete without this human factor.

Insomuch as but little effort was ever expended in studying the lion, a group of interested scientists and philanthropists in the Southwest pooled enough financial support to initiate a study of this beast which has now been three years in progress. The results of this study were published by the University of New Mexico Press, Bulletin 318 under the title, "A Preliminary Survey of the Mountain Lion." The following observations are in part taken from this bulletin and in part supplemented by material garnered since its publication.

Paramount among the burning issues of such an investigation stand the questions, "What is the lion's relation to domestic stock?" "What is the relation of the lion to game animals?" As a preliminary toward the solving of this first query, an analysis of lion meals was made, for the most part from dung specimens. These are deposited on typical "scrapes" which render them easy of identification and invariably contain hair which is distinctive of the kill represented. The game relations are more difficult of statistical study and come from two sources. First, observations of as many lions as possible and examination of their habits and modes of procuring food; and second, an analytical study, from a biological and anatomical standpoint, of game animals killed by lions. The record of the dung specimens has now mounted to 3,000 and of course gives a much more complete and yet just as certain a picture of the lion's food habits as stomach analysis, as the latter are so hard to procure. The following gives a list of the more important food items by percentages as evidenced by scatological and stomach examinations: Rocky Mountain mule deer (*Odocoileus hemionus macrotis*), 54 per cent, Sonora white-tailed deer and Arizona white-tailed deer (*Odocoileus couesi*), 28 per cent, Arizona porcupine (*Erethizon epixanthum couesi*), 5.8 per cent, Common cotton-tail rabbit (*Syl-*

vilagus nuttalli pinetis, *S. auduboni arizonae*, *S. auduboni minor*, *S. auduboni cedrophilus*), 4 per cent, Black-tailed jack-rabbit (*Lepus californicus eremicus*, *L. c. texianus*), 2 per cent, Domestic cattle (of several species), .5 per cent.

The remaining 5.7 per cent vary in different localities among the following interesting species: Texas or Mexican badger (*Taxidea taxus berlandieri*), Common striped skunk (*Mephitis estor*), Arizona gray fox (*Urocyon cinereoargenteus scotti*), Arizona coyote or Great Basin coyote (*Canis lestes*), Canadian, Pecos, Rio Grande beaver (*Castor canadensis mexicanus*), Southwestern or Sonoran beaver (*Castor canadensis frondator*), Prairie dogs of different species (*Cynomys*).

In addition to the above, there appear minor percentages of: Grasses (Various species), seeds (*Opuntia* and juniper have been identified), unknowns—this representing, it seems, immature specimens of rare occurrences of mammals whose hair is as yet difficult of identification. It is interesting to note the entire absence of any feather or bird kill of any kind whatsoever.

The two obvious facts in the above summary indicate an overwhelming majority of deer and an interestingly small count of domestic stock. It must be emphasized in connection with the above that every collecting station was in a sector heavily ranged by cattle, horses, sheep and goats. The opportunity was not lacking for an equal number of kills from the domestic categories.

There is no question that the mountain lion can and does kill economic animals upon occasion. It is the frequency of the occasion and circumstances which are in doubt. The bad name which the puma has received in popular narrative is far, however, from being justified. It was, in fact, the curious circumstance that a lion would often pass by easily procurable cattle or horses to secure more difficult deer which prompted the investigation.

The known deer-eating tendencies of the lion damned him from the start in the eyes of the game interests. Some game experts have, however, made public the opinion that a few lions might be of some good in a game community. This rather indefinite belief has seldom taken concrete form or expression heretofore. Likewise most sources state that a lion kills a deer a week and game departments base estimates of value on this guess. From records of the daily wanderings of over 200 lions, this is now judged too high and a deer a month would come closer to the mark.

As a part of this endeavor, a check was made on deer killed by rifles in the regular hunting season at the checking stations provided by the New Mexico Game Department. Here, deer were measured, examined, and weighed. Several interesting features immediately developed, such as differences in northern and southern counties in the same species, peculiarities of measurements in the same mountain range, etc. For this purpose, however, these measurements and observations on hunter-killed deer provided a basis of comparison and a cross-section of deer conditions in those areas, from whence the specimens came. From these same sections as many lion kills as possible were examined and measured in the same manner. This number of kills is disappointingly small, as most of the lions had made at least one meal from the kill before its discovery and many had been eaten to such an extent as to render them useless. Only eleven kills were sufficiently whole to permit of examination in the prescribed manner.

A careful comparison of the lion-killed deer with the statistics compiled on deer from other sources indicates that the lion-killed deer are in a special category. It must be emphasized at this point that such a small number of specimens gives a standard error of alarming proportions but it is nevertheless indicative that of these 11 deer, each of the 11 displayed characteristics to which its decease might be attributed. Among the most apparent of these ailments were prenatal injuries, hoof deformities, pronounced tick and bot fly infestations, and, most prevalent—malproportion of body and limb. It may be pure coincidence that extreme measurements of tarsus, front leg, body length, etc., are all to be found in the lion kill column. It would be premature to speculate that an animal which differs from its fellows in a longer body or shorter legs would be less liable

to survive. If this is not pure coincidence, it may be an interesting observation upon natural means for conforming a species to a norm.

Observations on lions' habits have already brought forth information too lengthy to set down within the confines of this paper. Size of the prey seems to make no difference as to availability to lions inasmuch as elk, large horses, or steers have been killed upon occasion. The ease of killing, on the other hand, appears to be dependent upon numerical abundance and especially the vulnerability of those subnormal or abnormal natural animals. It seems logical likewise that sheep, goats, calves or the like would fall into this class of vulnerables, rendered so by domesticity. The small percentage of the latter in the lion kill list is indicative then, perhaps of a special choice or propensity for the "natural" food.

That this propensity may become individual is illustrated by such specimens as the lion from Mingus Mountain, Arizona, which apparently lived on porcupines entirely, although deer were plentiful. Another lion observed for some weeks fed on rabbits. Also others have been reported which had developed a liking for sheep or cattle. It is these last perhaps which have cost the species its place among the chosen few to be preserved.

So, as in any other problem of ecology, a clarified view is apt to be lost in generalities. The common every-day generalities which have become established in lay and scientific minds alike have, perhaps, denied the predator his true place. It is out of keeping with modern ecological ideas to regard any part of fauna or flora as isolated.

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SOME FACTORS AFFECTING SLEET DAMAGE TO SHADE TREES ON THE SOUTHERN GREAT PLAINS

Soil moisture is an important factor in controlling tree growth within the southern Great Plains area.¹ The soil is often excessively dry because of the characteristic light rainfall coupled with the high rate of evaporation due to the high winds.² In northwestern Texas, western Oklahoma, and northeastern New Mexico a few woody species have been successfully located on carefully chosen sites where there is a considerable natural accumulation of moisture.³ Species best adapted to this area are those with deep-penetrating and wide-spreading root systems.⁴ In towns shade trees are somewhat protected from desiccation by buildings and other obstructions to surface wind currents, making possible a wider choice of species than on the open prairie. Shade trees on city lots and in municipal parks require much artificially added water over a greater portion of the year.

Severe sleet storms provide an additional hazard to woody plants in this section. A brief sleet storm may severely retard tree growth and development. Several factors control the extent of ice damage to trees. Injury may be expected to species with fine twigs

¹ Clark, E. R. 1934. A preliminary report of the growth and effectiveness of wind-breaks in the High Plains area of Oklahoma. [*Okla.*] *Panhandle Agr. Expt. Sta., Bull.* 55: 3-12.

² Johnson, F. R., and F. E. Cobb. 1926. Tree planting in the Great Plains region. *U. S. Dept. Agri., Farmers' Bull.* 1312.

³ Finnell, H. H. 1935. Prevention and control of wind erosion of High Plains soils in the Panhandle Area. *U. S. Dept. Agri. Soil Conserv. Serv.* (mimeographed pamphlet). 22 pp. *Amarillo, Texas.*

⁴ Bunker, M. T., and H. J. Thomson. 1938. Root development as a factor in the success or failure of windbreak trees in the southern High Plains. *Jour. Forestry* 36: 790-803.

due to the large surface area upon which ice may accumulate (Rogers; Croxton).⁵ Rogers has shown that the weight of accumulated ice varies in its ratio to the weight of the twig from 132:1 in American elm, *Ulmus americana* L., to 5:1 in white oak, *Quercus alba* L. Trees with brittle wood may suffer heavily from ice storms (Buttrick; Rogers, '23).⁶ The amount of stem taper, the symmetry, shape, and height of the crown, and the dominance of the tree have all been reported as factors related to ice storm damage to forest trees (Vorreiter, Haufe, Windirsch, DoBele, and Curtis, respectively).⁷ Rogers ('23) reported cottonwood, *Populus deltoides* Marsh., as a species highly susceptible to ice damage in Wisconsin. Croxton ('39) found that American elm and the maple, *Acer saccharinum* L., suffered most from a sleet storm in Illinois.

OBSERVATIONS

A severe sleet storm occurred in the city of Amarillo, Texas, on February 16, 1938. Records from the local United States Weather Bureau Station showed that the amount of precipitation in the form of sleet was 0.95 inches. The wind was from the north-northeast with an average velocity of 9 miles per hour during the time of sleet formation and with an average velocity of 8.5 miles per hour on the following day. Heavy accumulations of ice covered the branches for nearly 24 hours subsequent to the storm. Many branches were severely bent or broken from the weight of the ice. Few, if any, trees were completely destroyed.

In order to determine the extent of damage, a study was made of individual species of shade trees along several miles of city streets in Amarillo. The species observed were those most commonly planted in towns of the southern Great Plains area. The results of this study are presented in table I. Damaged trees were those showing noticeable evidence of limb breakage.

TABLE I. *The effect of sleet on the common ornamental and shade trees in Amarillo, Texas, February 16, 1938*

Species	Number of trees observed	Number of trees damaged	Per cent damaged
Elm, <i>Ulmus pumila</i> L. and <i>U. americana</i> L.	701	244	34.8
Ash, <i>Fraxinus lunceolata</i> Borkh.	492	1	0.2
Maple, <i>Acer saccharinum</i> L.	358	3	0.8
Poplar, <i>Populus deltoides</i> Marsh.	88	3	0.3
Sycamore, <i>Platanus occidentalis</i> L.	43	0	0.0
Catalpa, <i>Catalpa speciosa</i> Warder.	24	0	0.0
Locust, <i>Robinia pseudo-acacia</i> L.	34	0	0.0
Hackberry, <i>Celtis occidentalis</i> L.	11	0	0.0
Evergreens, <i>Juniperus</i> sp., <i>Pinus</i> sp.	51	0	0.0

⁵ Rogers, W. E. 1922. Ice storms and trees. *Torrey* 22: 61-63.

———. 1923. Resistance of trees to ice storm injury. *Torrey* 23: 95-99.

Croxton, W. C. 1939. A study of the tolerance of trees to breakage by ice accumulation. *Ecology* 20: 71-73.

⁶ Buttrick, P. L. 1922. Storm damage to Michigan forests. *Jour. Forestry* 20: 527-532.

⁷ Vorreiter, L. 1937. Bau- und Festigkeits-eigenschaften des Holzes der Glatzer Schneebergsichte. *Tharandter Forstl. Jahrb.* 88: 65-126; 235-285; 351-385.

Haufe, M. 1934. Die Eisbruchkatastrophe 1933/34 in Sachsen. *Deutsche Forstwirt* 16 (78): 835-839; (79): 847-849.

Windirsch, J. 1936. Der Aufbau des Waldbaumes nach statischer Grundlage. *Tharandter Forstl. Jahrb.* 87: 533-566.

Curtis, J. D. 1936. Snow damage in plantations. *Jour. Forestry* 34: 613-619.

DoBele, Fr. Eugene. 1935. Die Reureifbruchzone im Erzgebirge. *Tharandter Forstl. Jahrb.* 86: 565-650.

These data show conclusively that elm, the most commonly planted genus in this city, was most severely damaged by the ice. No attempt was made to distinguish between Chinese elm and American elm in this study, since the diagnostic twig characters were well concealed under the accumulated ice at the time the data were collected. Later observations showed that Chinese elm outnumbered American elm preponderantly throughout the entire city. Ice damage seems to be one deterrent to the use of Chinese elm in the Great Plains area. This species is successfully grown in windbreaks (Clark, '34; George; Wyoming State Report),⁸ and it is known to be drought resistant (Stiles and Melchers).⁹

It was noted that injured elm trees were more abundant on the south and west sides of the streets than on either the north or the east sides. The exact extent of damage on opposite sides of the same street was determined by studying the condition on each side of streets running from north to south and on each side of those running from east to west. The results are presented in table II.

TABLE II. *The effect of location on elm trees during the sleet storm of February 16, 1938*

Side of street	Small trees (less than 7 feet)		Medium trees (7-18 feet)		Large trees (over 18 feet)	
	Number observed	Per cent damaged	Number observed	Per cent damaged	Number observed	Per cent damaged
North	76	14.5	118	28.8	32	71.9
South	21	61.9	54	50.0	46	50.0
East	25	0.0	90	15.6	9	67.0
West	38	31.6	96	52.1	96	32.3

These data establish definitely the effect of location on sleet injury to shade trees. Trees on the north side of a street running from east to west were nearer protective buildings during this storm when a north-northeast wind prevailed than those on the south side of the same street. Likewise trees on the east side of a street running from north to south had more protection during the storm than those on the west side. Trees up to 18 feet in height were much better shielded from the winds than taller ones whose crowns were raised above the protective influence of the low buildings characteristic of Southwestern architecture.

One further observation was that when elm trees of the same height but of varying crown width grew on completely exposed sites away from buildings, the extent of sleet damage apparently varied with the spread of the crown. Sixty-two trees with an average crown width of 10 feet were damaged to the extent of 41 per cent as compared to 26 per cent damage to 57 trees whose crowns averaged 6 feet in width.

SUMMARY

Elm is the least tolerant to breakage during sleet storms of any of the observed shade trees of the southern Great Plains region.

Location of shade trees in respect to surrounding buildings is an important factor in preventing limb breakage due to the combined effect of ice accumulation and wind.

Elm trees with wide crowns appear to be less tolerant to sleet injury than those of

⁸ George, E. J. 1936. Growth and survival of deciduous trees in shelterbelt experiments at Mandan, North Dakota 1915-34. *U. S. Dept. Agri. Tech. Bull.* 496.

Wyoming Station Report. 1937. Shelterbelt Species, pp. 36, 38, 41.

⁹ Stiles, E. H., and L. E. Melchers. 1935. The drought of 1934 and its effect on trees in Kansas. *Kansas Acad. Sci.* 38:107-127.

the same height but with narrower crowns when both are totally exposed to wind following ice accumulation.

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BIOCLIMATOLOGY IN BIOLOGICAL ABSTRACTS

Men engaged in research in medicine, public health, ecology, agriculture, forestry, botany or zoology, geography, and other fields, will welcome the announcement that BIOLOGICAL ABSTRACTS is undertaking a more complete abstracting and segregation of the current research literature in bioclimatology and biometeorology. The section BIOCLIMATOLOGY-BIOMETEOROLOGY will appear within the section ECOLOGY in BIOLOGICAL ABSTRACTS, and will be under the editorship of Mr. Robert G. Stone of the Blue Hill Observatory, Harvard University.

The increasing interest in climatic and meteorological factors in their relation to biology, medicine, and agriculture is one of the significant trends of modern science. Ecologists have long appreciated the importance of temperature, humidity, radiation, barometric pressure, wind movement, and meteorological factors generally, as important factors in controlling the distribution and abundance of animals and plants. Foresters, horticulturists, and entomologists have likewise been concerned with the interrelationships of climatic and meteorological factors to the organisms with which they work. The developments of air conditioning and aviation have lately brought other important research groups into the field resulting in an increasing amount of research. This is often the work of individuals and groups not now in effective contact with biologists, and frequently appears in periodicals not commonly consulted by biologists.

In all civilized nations diverse research groups have sprung into being which, though they often devote much attention to the same fundamental natural forces, still work in practical isolation from each other, with a different background of training, and associations, belonging to different societies meeting at different times and places, publishing in different journals, reading different literature, investigating different types of things. These groups, however, are beginning to apply common ideas and common methods to the study of situations that are basically similar. For example, techniques and concepts derived from a study of the influence of weather factors on the spread of influenza or the common cold are likely to have a very high transfer value as applied to the study of the spread or survival of plant disease or economic insects. Conversely, it should be possible for research workers in the field of public health to make use of many findings of the entomologists, foresters, ecologists, plant pathologists, and other biological groups.

The abstracting journals of broad scope, like BIOLOGICAL ABSTRACTS, are admirably suited to the sort of synthesis of fundamental knowledge that this situation demands. In inaugurating this service BIOLOGICAL ABSTRACTS will be fulfilling one of the functions for which it was originally intended: that of providing an effective tool for research workers by co-ordinating the literature of border-line fields.

Under the sectional publication plan this material will be found, at present, not only in Section A, ABSTRACTS OF GENERAL BIOLOGY, but also under Section B, ABSTRACTS OF EXPERIMENTAL ANIMAL BIOLOGY, Section D, ABSTRACTS OF PLANT SCIENCES, and Section E, ABSTRACTS OF ANIMAL SCIENCES.

EDITOR-IN-CHIEF,
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